BEETLES AND SPIDERS AS INDICATORS OF RECOVERY ON

PRINCE OF WALES ISLAND, ALASKA

By

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BEETLES AND SPIDERS AS INDICATORS OF FOREST RECOVERY ON PRINCE OF WALES ISLAND, ALASKA

A

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Abstract

Commercial logging is among the most important disturbance factors affecting forest biota. An indirect effect of commercial logging is minimal understory within young even-aged forests, which can decrease forest biodiversity. To improve management of young even-aged forest stands within the Tongass National Forest (TNF), foresters are testing alternative forestry practices under the Tongass-Wide Young-Growth Studies (TWYGS). However, little is known about how the new thinning treatments included in the TWYGS will affect forest biota and the recovery of young even-aged forest stands as they transition back into old growth forests. To investigate the effects of thinned secondary growth on forest biota in the TNF on Prince of Wales Island, Alaska, I compared spider and beetle biodiversity in thinned secondary growth to old growth forest stands, clearcuts, and un-thinned secondary growth. Pitfall traps, Berlese funnels, and Lindgren© funnel traps were used to collect spiders and beetles in each forest type to compare species richness, diversity, and assemblages, as well as to identify possible ecological indicators within each habitat. I hypothesized that thinned secondary growth would have a mix of old growth and clearcut species and be further in the process of recovery than un-thinned secondary growth. I found that (1) spider and beetle species richness and diversity from thinned secondary growth were not significantly different from other forest treatments; (2) spider assemblages in thinned secondary growth were significantly different from other forest treatments, whereas beetle assemblages were not different; (3) spider and beetle assemblage structure was mainly influenced by Leaf Area Index (LAI) and; (4) spider and beetle ecological indicators of clearcuts and old growth stands were found within thinned and un-thinned

secondary growth stands. These findings support my hypothesis that thinned secondary growth would have both old growth and clearcut species; however, thinned secondary growth was not found to be further in the process of recovery than un-thinned secondary growth at the time of this study. Although thinned secondary growth was not further in the process of recovery, it did not adversely affect the biodiversity of spiders and beetles. My results suggest that logging on Prince of Wales Island can change spider and beetle assemblages, but it doesn't negatively impact species richness or diversity. Thinned secondary growth spider and beetle biodiversity may be in the process of recovery to the biodiversity seen in old growth forests. Therefore, spider and beetle biodiversity may resemble old growth forest biodiversity as LAI values increase with closing canopy in thinned secondary growth forest stands. In addition, a checklist of arthropods collected on Prince of Wales Island, Alaska, as part of this work, combined with records from other projects and publications, are included followed by a description of a new species I discovered, *Caurinus tlagu* Sikes & Stockbridge 2013 (Mecoptera, Boreidae, Caurininae).

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Chapter 1 Introduction

1.1 Commercial Logging Effects on Arthropods:

Commercial logging is considered one of the most significant anthropogenic disturbances of forests occurring today (McClellan, 2007). Logging practices such as clearcutting converts old growth forest stands into young even-aged stands, causing the decline of forest specialists (Willett, 2001). It is estimated that 87% (out of 331 imperiled or federally listed species) of invertebrate populations of concern are declining as a result of habitat loss (Stein, Kutner, & Adams, 2000). Some species such as *Agathidium pulchellum* (Coleoptera: Leiodidae) (an old growth forest specialist) are becoming endangered because of habitat loss caused by commercial logging (Laaksonen, Murdoch, Siitonen, & Varkonyi, 2010; Tykarski, Putchkov, & Mannerkoski, 2010). To address the potential loss of natural biodiversity including invertebrates, forest managers developed silvicultural practices regulating the 'establishment, growth, composition, health, and quality of forests' (Alaska Forest Resources and Practices Act, 2013; Deal, 2007; USFS, 2013). Managing post-harvest forest habitat is beneficial to invertebrates. Invertebrates influence many interactions within ecosystems because they are the most highly diverse and dominant group of animals (Kremen et al., 1993). Specifically, arthropods provide valuable ecosystem services such as pollination, nutrient cycling, and are vital sources of food for consumers (New, 1995). The loss of these essential services and interactions through commercial logging could negatively impact ecosystems.

1.2 Coastal Temperate Rainforests:

Forest management has mainly focused on highly productive ecosystems such as coastal temperate rain forests. Coastal temperate rain forests are unique and rare ecosystems comprising only 2-3% of temperate rain forests worldwide (Wolf, Mitchell, & Schoonmaker, 1995). Approximately 25% of the world's coastal temperate rain forest is in the Tongass National Forest (TNF) in Southeast Alaska (Dellasala, Hagar, Engel, & McComb, 1996). The TNF is the nation's largest national forest and encompasses ~17 million acres (McClellan, 2007) of highly productive old growth forest stands.

Productive old growth forest stands worldwide are the primary targets of commercial logging. Nearly 12% of the world's coastal temperate rainforest has been clearcut, resulting in the development of young even-aged forest stands following harvest (Wolf et al., 1995). In the 1950s, the TNF experienced intensive timber harvesting, creating ~ 430,000 acres of young even-aged stands (McClellan, 2007). These logging practices may be problematic for biodiversity because characteristics of young even-aged stands and old growth forest differ considerably.

1.3 Old Growth vs. Young Even-Aged Stands:

Old growth forest stands contain complex forest or habitat structures essential for a variety of wildlife and are valuable to many animals including arthropods (Deal, 2007; McClellan, 2007). Old growth stands are characterized by trees that are over 150 years old, have multi-layered canopies that allow sunlight to penetrate through the canopy, contain downed woody material, and have diverse understory vegetation (Dellasala et al., 1996). In contrast, young even-aged stands, which typically develop a closed

canopy 20-30 years after clearcutting, lack the structural habitat complexity characteristic of old growth stands (Deal, 2007). Young even-aged stands consist of trees that are less than 150 years old, with a single-layered canopy that allows little sunlight to filter through the canopy, permitting minimal understory vegetation growth on the forest floor (Alaback, 1984; Deal, 2007). Scarce understory vegetation conditions resulting from lack of sunlight on the forest floor in dense young even-aged stands (the stem-exclusion stage) can persist for over 100 years (Alaback, 1982). During the stem-exclusion stage, high competition for resources causes some trees to die and fall, creating gaps and allowing sunlight to penetrate through the canopy. However, even with increased sunlight, understory vegetation within young even-aged forest stands may not fully re-establish or resemble old growth forest vegetation for an additional 20-50 years (Alaback, 1982; Hanley, 2005). This lengthy period with little understory vegetation has been shown to have negative implications to wildlife depending on dense and diverse understory vegetation to survive (Deal, 2007).

1.4 TNF Management:

Extensive clearcutting in the TNF during the 1950s expanded the area of young even-aged stands, increasing the concern about enlarging the zones of forest in the stem-exclusion stage. During the 1990s, forest managers applied several techniques for managing young even-aged stands including gap-phase succession (removal of small groups of trees) and different thinning methods in the TNF (Deal, 2007; Hanley, Smith, & Gende, 2005; Hanley, McClellan, Barnard, & Friberg, 2013). However, most of the case study results were not reported because they 'lacked appropriate controls, replication, and random assignment of treatments' (McClellan, 2007). To study and

improve the management of young even-aged stands, TNF forest managers and researchers at the Pacific Northwest Research Station developed a new adaptive management program in 2001 called the Tongass-Wide Young-Growth Studies (TWYGS) (Hanley et al., 2013; McClellan, 2007). The main goal of TWYGS is to improve the habitat for old growth forest specialists by reducing the time period of the stem-exclusion stage (TWYGS, 2008). To achieve this goal, the TWYGS program prescribed thinning of dense young even-aged stands, increasing the availability of sunlight to the forest floor and stimulating the growth of understory vegetation. It is yet uncertain how forest biota have responded to these thinning treatments. Comparative studies between the TWYGS treatments and other forest habitats such as old growth stands are needed to evaluate whether these new practices are successful and should be implemented in the future.

1.5 Ecological Indicators:

One technique that researchers have used to compare the effects of different habitat alteration practices is the use of ecological indicator species (Maleque, Maeto, & Ishii, 2009). Ecological indicators are species that convey information about an ecosystem that is difficult to measure directly, such as its biodiversity or its rate of recovery after anthropogenic disturbances (Langor & Spence, 2006). Effective ecological indicators must be sensitive to changes in the environment that can be quantitatively measured such as changes in abundance within disturbed areas (Pearce & Venier, 2006). Although there is not a set of rules on how to identify groups of arthropods that could be potential ecological indicators, attributes of effective indicators should include a strong relationship between selected indicators and disturbance factors

of interest (i.e. habitat types) and applying these chosen indicators for future monitoring of biotic response to disturbances (Langor & Spence, 2006). In areas disturbed by logging practices, many researchers have studied well-known groups such as vertebrates (Dellasala et al., 1996) or plants (McClellan, 2007) as ecological indicators of recovery (Langor & Spence, 2006). Arthropods as indicators of ecological change have been studied less frequently because expert knowledge to make accurate species level identifications is required (Langor & Spence, 2006; Kremen et al., 1993).

Despite this difficulty, terrestrial arthropods are efficient ecological indicators because they are one of the most diverse components of terrestrial ecosystems. Additionally, arthropods occupy a variety of functional niches and microhabitats with high site specificity; thus, they respond quickly to changes in their environment (Dollin, Majka, & Duinker, 2008; Kremen et al., 1993). Arthropods are also relatively easy to collect compared to vertebrates. Hundreds of species can be sampled for the same effort it takes to sample one or a few vertebrate species. Another reason terrestrial arthropods are successful ecological indicators is that few species embark on wide-ranging migrations. This ensures that any deviation in resident populations of arthropods reliably reflects changes in their local habitat during summer seasons (Langor & Spence, 2006).

Arthropods have been evaluated successfully as ecological indicators in several studies to investigate effects of different logging practices on forest biota in countries with similar latitudes to Alaska. For example, studies in Canada and Finland examined different families or functional groups of beetles and spiders as indicators in order to evaluate the effects of clearcutting and different kinds of forest management on forest

biota (Dollin et al., 2008; Klimaszewski, Langor, Work, Hammond, & Savard, 2008; Matveinen-Huju & Koivula, 2008; Pohl, Langor, Klimaszewski, Work, & Paquin, 2008; Work et al., 2008). Previous studies have found high species richness of arthropods after clearcutting, because open habitat species invade the disturbed areas, while low numbers of some forest specialists persist (Niemelä, Langor, & Spence, 1993; Pohl et al., 2008). As harvested areas regenerate, forest specialists begin to return. Nevertheless, some forest species may never re-establish (Pearce & Venier, 2006). Although there have been several studies on how harvesting treatments affect arthropods, there has been little research using arthropods as ecological indicators to evaluate the effects of thinning young even-aged forest stands on forest biota (Huhta, 1965; Schowalter, Zhang, & Rykken, 2003).

Most studies have evaluated only one particular group, order, or family of arthropods as ecological indicators. Some researchers consider the ecological loss of one or more single species to be less significant than losing 'species interactions and their ecological functions' (Levin & Levin, 2002; Soulé, Estes, Berger, & Del Rio, 2003). Therefore, a management program that uses a multi-taxon approach may have greater potential to conserve invertebrate species, their interactions, and their habitats (Soulé et al., 2003). Both spiders and beetles have been separately evaluated as effective ecological indicators in previous studies. Although spiders are exclusively predators, their species richness and habitat diversity is high, and beetles are the most ecologically and species rich order of animals. An evaluation of using both spiders and beetles as ecological indicators in the TWYGS program may provide unique and powerful insights on these habitats and their recovery.

Forest recovery is the process of forests returning to an old growth state after a disturbance. After a clearcutting disturbance, managers are interested in how fast forests recover and how different forestry treatments affect recovery. The process of recovery can be evaluated with the use of ecological indicators by identifying indicators that are highly associated with certain habitat types and/or stages of recovery. In this study, I used ecological indicators to evaluate the recovery of thinned young even-aged stands. If mostly old growth indicators are found in thinned young even-aged stands, then these stands would be considered in the later stages of recovery. If mostly clear cut indicators are found in thinned young even-aged stands, then these stands would be considered in the early stages of recovery. These results can used to understand the level of recovery of thinned young even-aged stands in order to evaluate the effect of thinning on young even-aged stands.

1.6 Goal of Study:

To evaluate how spiders and beetles are affected by the TWYGS experiment and evaluate their value as ecological indicators, I compared samples of spiders and beetles from thinned young even-aged forest stands (thinned secondary growth) to those from old growth forest stands, un-thinned young even-aged forest stands (un-thinned secondary growth), and clearcuts. Spiders and beetles were collected from each treatment to: (1) compare species richness, diversity and assemblages and (2) determine if there are any species that are completely or highly associated with any one treatment, representing ecological indicators for specific habitats. Identified ecological indicators were used to measure the level of recovery for thinned secondary growth. I hypothesized that thinned secondary growth would have a mix of old growth (forest

specialists) and clearcut (open habitat specialists) indicators. In addition, I hypothesized that thinned secondary growth would be further in the process of recovery showing spider and beetle assemblage structures closer to or not significantly different than old growth compared to un-thinned secondary growth.

Results for the study of biodiversity in the Tongass National Forest are described in the main chapter of this thesis followed by an arthropod checklist for Prince of Wales Island, Alaska (Appendix A). This checklist includes records of arthropods collected from this and other studies with specimens in UAM, records from a literature search, and a new species, *Caurinus tlgau* Sikes & Stockbridge 2013, (Mecoptera, Boreidae, Caurininae) that I discovered. The new species is described in Appendix B.

Chapter 2 Materials and Methods

2.1 System Descriptions:

2.1.1 Study Area:

I conducted my study in the Tongass National Forest (TNF) on Prince of Wales Island, Alaska, USA (55.886836N, 132.966592W ± 15 km; POW; Fig. 1). Prince of Wales Island has an annual mean temperature of 10°C and an annual mean precipitation of 280 cm (Schultz & DeSanto, 2006). The TNF is coastal rainforest dominated by western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*) with lesser amounts of Red Alder (*Alnus rubra*), Alaska yellow cedar (*Chamaecyparis nootkatensis*), red cedar (*Thuja plicata*), and lodgepole pine (*Pinus contorta* var. *contorta*). Common understory vegetation includes blueberry (*Vaccinium ovalifolium*), salmonberry (*Rubus spectabilis*), devil's club (*Oplopanax horridus)*, false azalea (*Menziesia ferruginea*), skunk cabbage (*Lysichiton americanus*) and several species of ferns (nomenclature follows Hultén, 1968).

2.1.2 Tongass-Wide Young-Growth Studies Sites:

The Tongass-Wide Young-Growth Studies (TWYGS) included sites that were widely distributed throughout the TNF. However, most of their sites were established on the North side of POW where there were many young even-aged forest stands due to intensive logging (Farr & Harris, 1979). TWYGS included five different thinning methods that were established from 2002 to 2006. Each thinning method had 19-23 replicates and an average size of 23 acres. In addition, every thinning treatment site was paired with an adjacent control of un-thinned secondary growth.

2.2 Study Design:

To evaluate species assemblages I used three of the five different TWYGS thinning treatments and their paired controls (Fig. 1 A,B,C,D). The thinning treatments I used were 15 to 35 years old at the time of my study and thinned to a density of trees that ranged from 135 – 222 trees per acre (TWYGS, 2008). I combined three different thinning treatments into one (thinned secondary growth) for data analysis to obtain enough replicates per treatment. Furthermore, I included two additional treatments, old growth stands and clearcuts (Fig. 1 E,F; McClellan, 2007). Both old growth stands and clearcut sites are located on the northern side of POW close to the TWYGS sites (Fig. 2) and were chosen based on accessibility to road systems. Each of the four treatments (old growth, clearcut, thinned secondary growth, and un-thinned secondary growth) had six replicates for a total of twenty-four sites (Table 1). Sampling was conducted from mid-May to mid-August from 2010 to 2011 and samples were taken from each site in two-week intervals for a total of six sampling intervals per field season.

To investigate the recovery process of thinned secondary growth forest stands, all species of beetles (excepting aleocharine staphylinids) and spiders were used to compare assemblages across treatments. Consistently abundant species in specific treatments were evaluated as potential indicators of forest recovery. I chose to use adult beetles and spiders because they were used successfully as ecological indicators in past studies (Klimaszewski et al., 2008; Willett, 2001) and immatures are often unidentifiable.

Figure 1. Treatments and Controls used on Prince of Wales Island, Alaska. **A** Thinned secondary growth with 14 ft. spacing **B** Thinned secondary growth with 16 ft. spacing **C** Thinned secondary growth with 18 ft. spacing **D** Un-thinned secondary growth **E** Old growth **F** Clearcut.

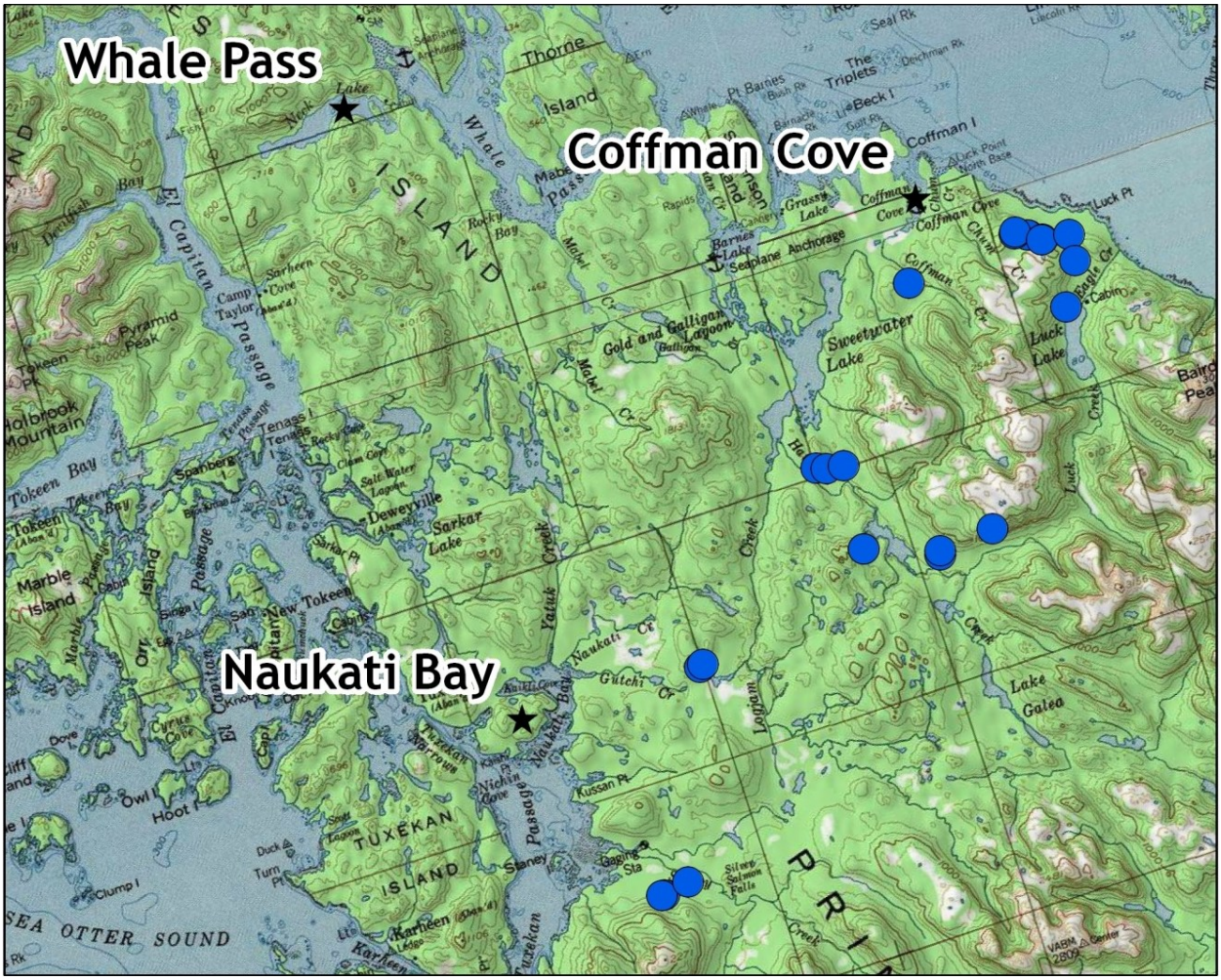

Figure 2. Locations of all 24 study sites on Prince of Wales Island, Alaska. Blue dots indicate study sites (Created by Nick Lisuzzo, USFS FHP Region 10).

Table 1. List of treatment sites, names used in analyses, and locations on Prince of Wales Island Alaska.

Site Name	Replicate Name	Treatment	Latitude	Longitutde
POW Coffman Cv	Thin 1	Thin: 14x14	55.97950	-132.86256
POW Coffman Cv	2nd Gro. 1	2nd growth	55.98053	-132.86070
POW Hatchery Ck. 1	Thin 2	Thin: 14X14	55.92524	-132.95054
POW Hatchery Ck. 1	2nd Gro. 2	2nd growth	55.92654	-132.95645
POW Hatchery Ck. 1	Old Gro. 1	Old growth	55.92444	-132.93938
POW Hatchery Ck. 2	Thin 3	Thin: 18X18	55.89356	-132.94370
POW Hatchery Ck. 2	2nd Gro. 3	2nd growth	55.89356	-132.94370
POW Hatchery Ck. 4	Thin 4	Thin: 18X18	55.88433	-132.89734
POW Hatchery Ck. 4	2nd Gro. 4	2nd growth	55.88285	-132.89795
POW Hatchery Ck. 4	Old Gro. 2	Old growth	55.88602	-132.86070
POW Staney Ck.	Thin 5	Thin: 16X16	55.79726	-133.13630
POW Staney Ck.	2nd Gro. 5	2nd growth	55.79723	-133.13467
POW Staney Ck.	Old Gro. 3	Old growth	55.79901	-133.11782
POW Staney Ck.	Clearcut 1	Clearcut A	55.87134	-133.06755
POW Staney Ck.	Clearcut 2	Clearcut B	55.87200	-133.06523
POW Luck Pt.	Thin 6	Thin: 16X16	55.98261	-132.77986
POW Luck Pt.	2nd Gro. 6	2nd growth	55.98256	-132.77943
POW Luck Pt.	Clearcut 3	Clearcut 1A	55.98452	-132.78786
POW Luck Pt.	Clearcut 4	Clearcut 1B	55.98497	-132.78700
POW Luck Pt.	Clearcut 5	Clearcut 2A	55.97953	-132.77156
POW Luck Pt.	Clearcut 6	Clearcut 2B	55.97939	-132.77216
POW Luck Rd.	Old Gro. 4	Old growth 1	55.97805	-132.75456
POW Luck Rd.	Old Gro. 5	Old growth 2	55.96855	-132.75615
POW Luck Rd.	Old Gro. 6	Old growth 3	55.95347	-132.77080

2.3 Field and Laboratory Methods:

2.3.1 Collection of Beetles and Spiders:

I used routine beetle and spider sampling methods to collect a wide variety of species (e.g. Willett, 2001; Pohl et al., 2008; Work et al., 2008). Three types of trapping methods were used: two passive (Lindgren© funnels and pitfall traps) and one active (Berlese funnels). To control for edge effects, traps were haphazardly set by walking approximately 100 meters into each site. All traps used Sierra© brand low-toxicity propylene glycol-based antifreeze to kill and preserve arthropods.

Two Lindgren© funnels were set at each site. These funnels target tree-associated beetles and are composed of a series of black plastic funnels attached one above the other which, when hung, mimics a tree. Beetles that collide with the funnels, fall into a catchment below the bottom-most funnel and are preserved. To ensure that rain water did not dilute the preservative, 5x4 ft. plastic rain roofs were hung above each Lindgren© funnel. In addition, I also baited the Lindgren© funnels with Alpha Scents (1089 Willamette Falls Drive, West Linn, OR 97068, USA) ethanol lures to attract beetles.

Four pairs of pitfall traps were placed at each site to capture ground-dwelling arthropods. A pair of pitfall traps consisted of two 9 oz. plastic cups that were placed in the ground one foot apart with the lip of the cups even with the ground or slightly below ground level. To maximize arthropod catch, a plastic ruler acting as a barrier was placed between the two plastic cups. Arthropods that hit the barrier usually followed the barrier until they fell into either plastic cup (Hansen & New, 2005). Plastic plates were

used as rain roofs above each trap. To collect flying arthropods, the plates were elevated ~ two inches above the ground by inserting two 6" plastic Raptor© nails on opposite sides into the lip of the plate and placed into the ground above each plastic cup (Work, Buddle, Korinus, & Spence, 2002).

Berlese funnels were used to obtain leaf-litter dwelling arthropods. I collected ~ $1m^2$ of leaf litter from each site once every two weeks. The leaf litter was sifted to concentrate the living matter into a smaller volume, placed onto a mesh screen within a Collapsible BioQuip© brand (2321 Gladwick St., Rancho Dominguez, CA 90220, USA) Berlese funnel, and heat was applied from a 40 watt light bulb (Kroger brand, 450 lumens) above the sample. The microfauna retreated from the heat by digging downwards, eventually falling through the mesh screen into a catchment below. Berlese funnels were run for 48 hours per sample, which was enough time to dry out the litter sample.

2.3.2 Vegetation:

To evaluate understory and overstory vegetation, I conducted surveys at each site following protocols similar to the TWYGS methods (TWYGS, 2008). For each vegetation survey, four 10 meter transects radiating from a single random sampling point in each of the cardinal directions were set for each site. To estimate understory vegetation percent cover, I measured occurrence in centimeters and identified vascular plants along each transect. To characterize overstory vegetation, I measured the diameter at breast height (DBH), basal area (BA), and total height for each tree species within each of the four quadrants defined by the transects. Within the un-thinned

secondary growth sites, all trees within each of the transect quadrants were counted to obtain density; however, only ten randomly selected trees per transect quadrant were measured for height, DBH, and BA. This was due to the high density of trees at this particular type of site; moreover, all the trees in this habitat generally have the same height and DBH. To measure the amount of sunlight that can penetrate through the canopy at each site, I used the linear sensor AccuPAR© ceptometer (Decagon Devices, 2365 N.E. Hopkins Ct., Pullman, WA 99163, USA). AccuPAR© recorded photosynthetically active radiation (PAR) that passed through the canopy. These AccuPAR© measurements were used to calculate LAI. Higher values of DBH, BA, and LAI, correspond to less sunlight that can penetrate through the canopy to the forest floor.

2.3.3 Laboratory:

Field samples were processed at the University of Alaska Museum in Fairbanks, Alaska. I sorted the beetles and spiders from by-catch for each sample. A unit-tray's worth of beetles for each species were mounted on #3 stainless steel pins (Bioquip© brand), with the remainder stored in 70% ethanol in Nalgene (Fisher Scientific, Bishop Meadow Rd., Loughborough, Leicestershire, LE11 5RG UK) 20 mL vials. All spiders were stored in 70% ethanol in Nalgene vials by sample with rare species transferred to 1 dram glass vials (Bioquip© brand) (one species per vial). All mounted beetles and glass-vialed spiders were given unique barcodes linking them to their Arctos (Arctos, 2014; http://arctos.database.museum/home.cfm) database records. All specimens in Nalgene vials, which often represented multiple species, were also databased but shared the single barcode of the Nalgene vial. All by-catch was saved and databased. I

identified beetles and spiders to species or morpho-species. Spider identifications were determined by specialist Jozef Slowik and beetles difficult to identify were loaned to experts James Bergdahl (Carabidae), Patrice Bouchard (Curculionidae), Stelios Chatzimanolis (Staphylinidae: Staphylininae), Anthony Davies and Milt Campbell (Staphylinidae: Micropeplinae, Steninae, Tachyporinae), Olaf Jaeger (Byrrhidae), Richard Leschen (Cryptophagidae), Paul Johnson (Elateridae), Alexey Shavrin (Staphylinidae: Omaliinae), Paul Skelly (Scarabaeidae: Aphodiinae), and Margaret Thayer (Staphylinidae: Omaliinae). The classification of spiders was based on Platnick (2014). The classification of beetles was based on Arnett and Thomas (2001) and Arnett, Thomas, Skelly, and Frank (2002). All beetle and spider data were recorded in the database Arctos and are available online to the public at http://arctos.database.museum/project/effects-of-forestry-practices-on-ecological-indicator-species-in-the-tongass-national-forest-prince-of-wales-island-alaska.

2.4 Statistics:

2.4.1 Beetle and Spider Data:

I tested for differences between four treatments: thinned secondary growth, old growth, un-thinned secondary growth, and clearcuts. For all beetle analyses, I combined data from both field seasons 2010 and 2011 to look for statistical differences in the overall species richness, diversity, and assemblage differences between treatments (I was not interested in looking for variation from year to year). Spider analyses only included 2010 data because funding was lacking for expert identification for samples collected in 2011.

2.4.2 Species Richness and Diversity: Total species richness and diversity indices for spiders and beetles were calculated in Microsoft Excel 2010 (Microsoft Excel, Redmond, Washington). Species richness estimates were calculated in EstimateS© 8.2 (Colwell, 2013). The total numbers of species (species richness, S) collected were summed for each treatment. The average number of species collected for each treatment was calculated by summing the number of species collected from the six replicate sites per treatment and taking the average. The total and average numbers of species collected per treatment were compared to species richness estimates from EstimateS© to determine if the number of species collected per sample and total number of species collected (S) per treatment was close to the actual number of species that inhabit the areas. I estimated species richness for each forest type using sample-based rarefraction curves or accumulation curves (Sobs) and Chao1 estimates with EstimateS. If the number of species collected per sample from each treatment was close to the species richness estimates for each treatment, then I concluded that I thoroughly sampled each treatment. In addition, to assess the redundancy of the collection methods used, I compared the number of species collected and their abundance by each trap type using matched abundance plots made in Microsoft Excel.

To measure diversity across the different habitats, I used the Shannon's Diversity Index and Shannon's Equitability Index (performed in Microsoft Excel 2010) (Warwick, Clarke, & Suharsono, 1990a; Warwick, Platt, Clarke, Agard, & Gobin, 1990b). The Shannon Diversity Index is a composite, based on species abundance or percentage of individuals among species, and number of species present within a given habitat. The

Index increases with either increasing evenness of species composition or increasing numbers of species. The Shannon's Equitability Index directly measures evenness of species composition. If there are relatively similar numbers of individuals collected for each species found in a habitat, then the species composition with that habitat is said to be even. If one species is highly abundant and many species are rare, then the habitat is said to be uneven.

One-way ANOVA and post-hoc paired t-tests (if ANOVA was significant) (performed in Microsoft Excel 2010) were used to detect differences between species richness (S), Shannon's Diversity Index and Shannon's Equitability Index between forest treatments (species richness, Shannon's Diversity, and Shonnon's Equitablity values were calculated for each replicate site (6 sites per treatment) to run an ANOVA and t-test for each treatment). For multiple comparisons, the Bonferroni correction was used to re-calculate alpha. A normal distribution was used to calculate 95% confidence intervals in Excel and these were used to look for differences in species richness estimates (Sobs, Chao1) between forest treatments.

2.4.3 Assemblages: All analyses for the multivariate community data were performed in the statistical software program R version 2.15.0 (R Development Core Team, 2012) with VEGAN and MASS statistical packages. Spider and beetle data were standardized because there were different numbers of samples taken from each site in 2010, whereas the number of samples taken from each site in 2011 was equal. To standardize the data, the number of individuals per species was divided by the total number of individuals collected for each site and multiplied by 100 in order to get the

percent of total abundance accounted for by each species (Clarke & Warwick, 2001). Spider and beetle abundance data were also log (x+1) transformed to down-weight the influence of highly abundant species, allowing rare species to also influence the outcome.

To compare spider and beetle assemblages among the four different treatments, I used Non-metric Multidimensional Scaling (NMDS) (Clarke & Warwick, 2001). NMDS is an indirect gradient ordination method that captures overall differences and similarities in community structure by mapping sites in multidimensional space. To estimate similarities among sites, I used the Bray-Curtis coefficient (Clarke & Warwick, 2001). This coefficient is not biased towards zeroes in a species data matrix. Using a coefficient that is biased towards zeroes would group sites as being similar due to joint absences (Clarke & Warwick, 2001). The spider and beetle species matrix contains many zeroes; therefore, using the Bray-Curtis coefficient is appropriate.

I tested for differences in spider and beetle assemblages using the ADONIS function in R, which is equivalent to a Non-Parametric MANOVA (NPMANOVA). The Bonferroni correction was used for multiple comparisons. If habitats were found to be significantly different in assemblages, I determined which species were responsible for those differences by using SIMPER analysis in R. SIMPER is an exploratory analysis that looks at the average contribution from each species to the total dissimilarity between pairs of significantly different habitats (Clarke & Warwick, 2001). Species that consistently (low standard deviation) had a high average contribution to the total dissimilarity between habitats were considered a good discriminating species. In

addition, species that were consistently found in high numbers in a specific treatment were considered to be highly associated with that particular habitat.

2.4.4 Feeding Groups: To determine whether certain feeding groups were significantly more abundant in particular treatments, I categorized all spider and beetle species by their main feeding group using the following references: Arnett & Thomas, 2001; Arnett et al., 2002, Bradley, 2013; BugGuide, 2014; Dondale, 1992; Dondale & Redner, 1978, 1982, 1990; Dondale, Redner, Paquin, & Levi, 2003; Hancock & Hancock, 2005; Levi & Levi, 1990; White, 1963. Because all spiders are carnivorous, spiders were also categorized as web builders (sit and wait predators) or either diurnal or nocturnal active predators. Beetle species were assigned to their feeding groups: carnivores, detrivores, fungivores, herbivores, and omnivores. Little is known about the feeding habits of some species; therefore those species were assigned to the dominant feeding habit of their genus or family. NMDS analyses were conducted in R using the VEGAN and MASS statistical packages to compare feeding groups by forest type. NPMANOVA was used to look for statistical differences between feeding groups.

2.4.5 Linking Arthropod Biotic Structure to Vegetation Variables:

To determine whether vegetation variables measured in the field could explain spider and beetle biotic structure and feeding group composition in the NMDS ordination plots, I used a univariate approach by correlating each vegetation variable to the NMDS axes in R using Spearman's correlation coefficient (Clarke & Warwick, 2001). Vegetation variables included height of trees, DBH, BA, LAI, and percent of understory vegetation cover. A vegetation correlation to the arthropod biotic structure of 0.5 was

considered to be a good fit (Clarke & Warwick, 2001). In addition, I also graphed overlays of the vegetation data for each variable onto the NMDS ordination plots. Higher vegetation variable values are graphed on the NMDS plot with larger circles, whereas lower vegetation variable values are graphed with smaller circles.

To explore how different combinations of vegetation variables correlate to beetle and spider biotic structure, I used the multivariate method BIOENV in R. BIOENV looks for maximum correlations between arthropod and vegetation matrices. A Spearman's correlation of 0.5 was considered a good fit between vegetation and arthropod community structure.

Chapter 3 Results

3.1 Species Richness and Diversity:

3.1.1 Spiders: A total of 4,805 adult spiders representing 59 species were collected in 2010 (Appendix A). Clearcuts yielded the highest total numbers of species (species richness, S), whereas un-thinned secondary growth yielded the lowest total number of species (S) collected (Table 2, Fig. 3A). Thinned secondary growth produced the highest total number of individuals, while clearcuts yielded the smallest total number of individuals collected. However, there were no significant differences between treatments in either average species richness or the average number of individuals collected (Table 2). Mean sample-based rarefied species richness estimates (Sobs) and mean total species richness estimates (Chao1) were higher than the average number of species collected, but lower than the total number of species (S) collected for each treatment. Therefore, adequate sampling of spider species for the different treatments was accomplished. Chao1 total species richness estimates were significantly higher in clearcuts compared to thinned secondary growth. Shannon's diversity (H) and Shannon's equitability (J) indices were not significantly different between treatments.

Table 2. Summary values for diversity analysis of spiders in thinned secondary growth (Thins), old growth, un-thinned secondary growth (2nd growth), and clearcuts. Number of individuals, species, average species, H, and J in habitats were significantly different if P < 0.008 with the Bonferroni alpha correction. Sobs and Chao1 estimates were significantly different if CI's did not overlap.

	Forest Treatments			
	Thins	Old growth	2nd growth	Clearcut
Number of Adult Individuals (n)	1616	1023	1237	929
Total Number of Species (S)	36	39	34	46
Average Number of Species (S)	21.5 (19.8, 23.2)	19.7 (17, 22.4)	19 (16.2, 21.8)	21 (17.6, 24.4)
Rarefied Species Richness Estimate (Sobs)	28 (20.6, 35.4)	35 (27.8, 42.2)	22 (14.8, 29.2)	35 (26.4, 43.6)
Total Species Richness Estimate (Chao1)	31.89 (31.4, 36.7)[b]	36.55 (33, 54.3)[ab]	31.37 (29, 45.3)[ab]	41.4 (37.9, 58)[a]
Shannon's Diversity Index	1.80 (1.5, 2.1)	1.96 (1.8, 2.1)	1.94 (1.8, 2.1)	2.05 (1.8, 2.3)
Shannon's Equitability Index	0.59 (0.5, 0.7)	0.66 (0.6, 0.7)	0.66 (0.6, 0.7)	0.68 (0.6, 0.8)

• Sobs, Chao1, H, and J values are means with 95% confidence intervals (CI's) in parentheses
• The symbols [a] and [b] indicate significant differences in values between forest treatments. Treatments that share the same symbol are not significantly different.

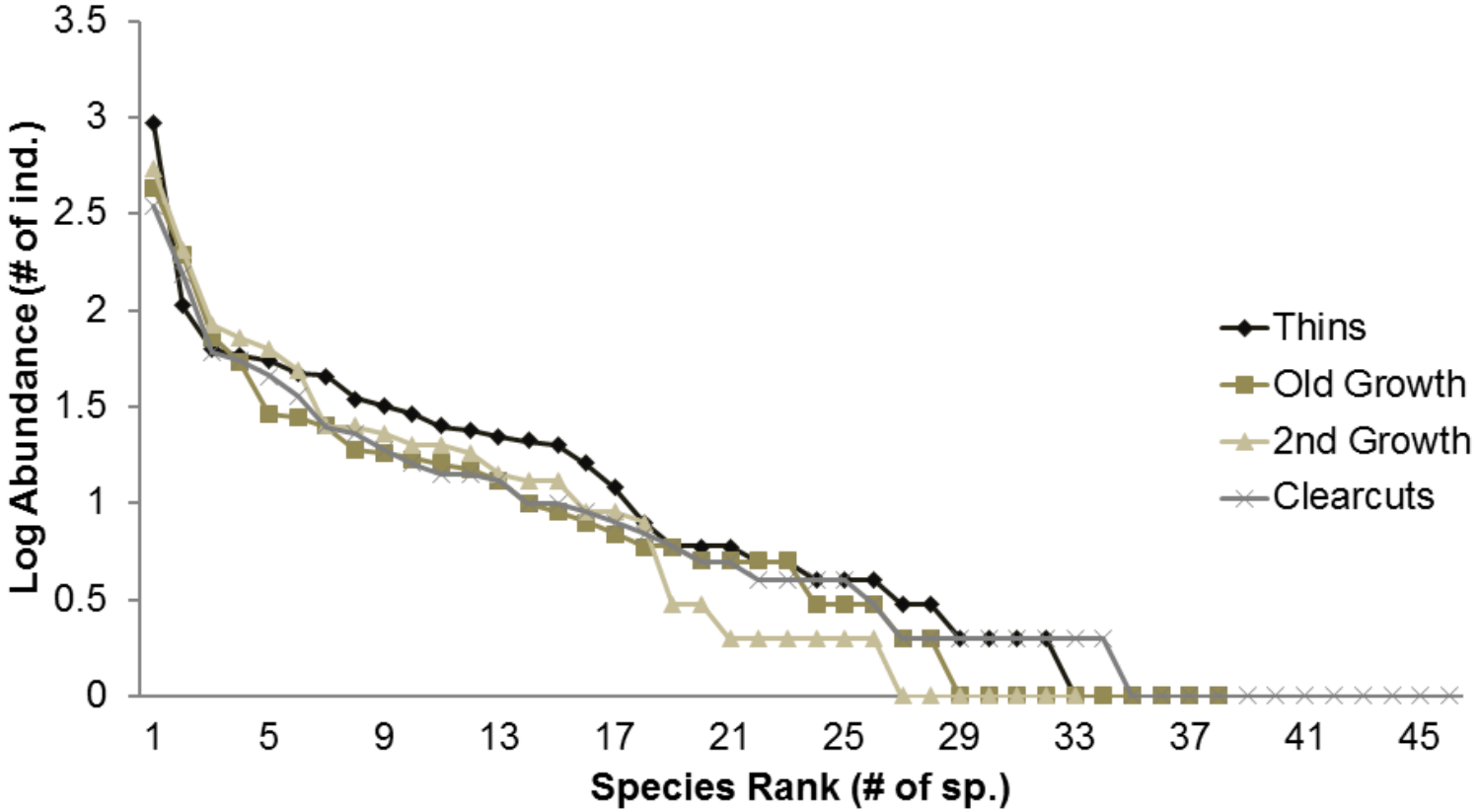

Figure 3A. Log (base 10) of relative abundance vs. species rank for spiders in thinned secondary growth (thins), old growth, un-thinned secondary growth (2nd growth), and clearcuts. Species rank is the number of species per forest type and abundance is the number of individuals per species log transformed. The highest abundant species (ranked 1) for all habitats is *Cybaeus reticulatus*.

3.1.2 Beetles: A total of 23,574 adult beetles representing 212 species were collected in 2010 and 2011 (Appendix A). The highest total numbers of species (S) and total individuals were found in clearcuts, whereas the lowest total numbers of species and total individuals were collected in un-thinned secondary growth (Table 3, Fig. 3B). Thinned secondary growth yielded the second highest average number of species collected, but this was not significantly different from other treatments. Clearcuts and old growth yielded a significantly higher average number of species (61 [two-tailed t-test, $t = 2.23$, $df = 10$, $P < 0.004$] and 20 [two-tailed t-test, $t = 2.23$, $df = 10$, $P < 0.009$] more species, respectively) compared to un-thinned secondary growth. However, there were no significant differences in the total number of individuals collected between treatments (Table 3). Mean Sobs and Chao1 species richness estimates calculated in EstimateS were higher than the average number of species collected, but lower than the actual number of species (S) collected for each treatment except thinned secondary growth. The Chao1 estimate for thinned secondary growth was higher than the actual number of species collected; however, the number of species collected in thinned secondary growth was within Chao1 estimated 95% confidence intervals. Therefore, sufficient sampling of beetle species for all treatments was achieved. Clearcuts contained the highest number of species (S, Sobs, Chao1), but had the lowest Shannon's diversity (H) and Shannon's equitability (J) indices. Although H and J differences were found to not be significantly different between treatments, the high species richness of clearcuts appears somewhat uneven (low J index and causing a decrease in H index).

Table 3. Summary of values for diversity analysis of beetles in thinned secondary growth (Thins), old growth, un-thinned secondary growth (2nd growth), and clearcuts. Number of individuals, species, average species, H, and J in habitats were significantly different if P < 0.008 with the Bonferroni alpha correction. Sobs and Chao1 estimates were significantly different if CI's did not overlap.

	Forest Treatments			
	Thins	Old growth	2nd growth	Clearcut
Number of Adult Individuals (n)	5449	5510	4270	8345
Total Number of Species (S)	134	131	111	172
Average Number of Species (S)	68.7 (59, 78.3)[ab]	70.7 (64.3, 77)[a]	56.8 (51.1, 62.5)[b]	85 (70.8, 99.2)[a]
Rarefied Species Richness Estimate (Sobs)	128 (113.7, 142.3)[b]	98 (83.7, 112.3)[c]	92 (77.8, 106.2)[c]	165(148.2,182)[a]
Total Species Richness Estimate (Chao1)	139 (127.3, 172.4)[ab]	124.3 (117.9, 145)[bc]	104.4 (99, 123)[c]	169(160,193.3)[a]
Shannon's Diversity Index (H)	2.7 (2.4, 2.9)	2.7 (2.5, 2.8)	2.7 (2.5, 3)	2.6 (2.4, 2.8)
Shannon's Equitability Index (J)	0.63 (0.57, 0.69)	0.63 (0.58, 0.67)	0.68 (0.62, 0.74)	0.58 (0.53,0.63)

• Sobs, Chao1, H, and J values are means with 95% confidence intervals (CI's) in parentheses
• The symbols [a] ,[b] , and [c] indicate significant differences in values between forest treatments. Treatments that share the same symbol are not significantly different.

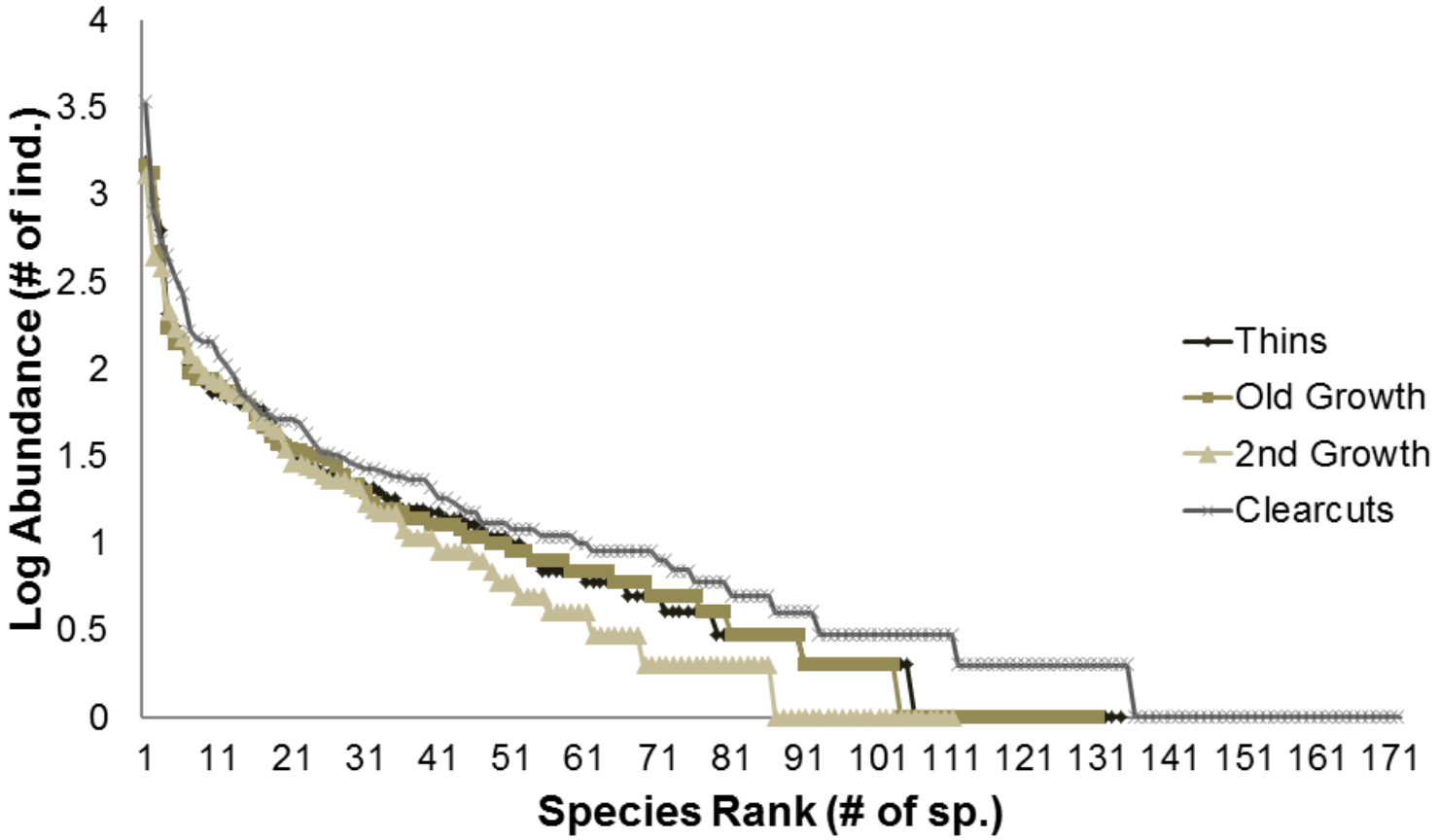

Figure 3B. Log (base 10) of relative abundance vs. species rank for beetles in thinned secondary growth (thins), old growth, un-thinned secondary growth (2nd growth), and clearcuts. Species rank is the number of species per forest type and abundance is the number of individuals per species log transformed.

3.1.3 Spiders and Beetles: The positive correlation between spider and beetle species richness by treatment shows that spider and beetle species richness was generally higher in clearcuts and lower in un-thinned secondary growth (Fig. 4). However, the correlation is weakly positive ($R = 0.407$, $df = 22$, $p = 0.048$).

Matched abundance plots were used to determine the number and abundance of species caught using pitfall traps, Berlese funnels and Lindgren© funnels (Fig. 5A, B, C, D, E, F). The trapping method on the right side of each graph shows the number of species (represented by each line) and the abundance of each species (log transformed) collected by that specific trap. The left side of each graph represents the overlap of species and their abundances caught by a different trap method. There was a large overlap in species caught by Berlese funnels and pitfall traps, but pitfall traps had higher abundances of the same species caught (Fig. 5A) and collected more total species than Berlese funnels (Fig. 5C). Lindgren© funnels collected several species not collected from Berlese and pitfall traps (Fig. 5E, F). These results indicate that Lindgren© funnels and pitfall traps are the most time-efficient trapping methods with the least redundancy in species collected.

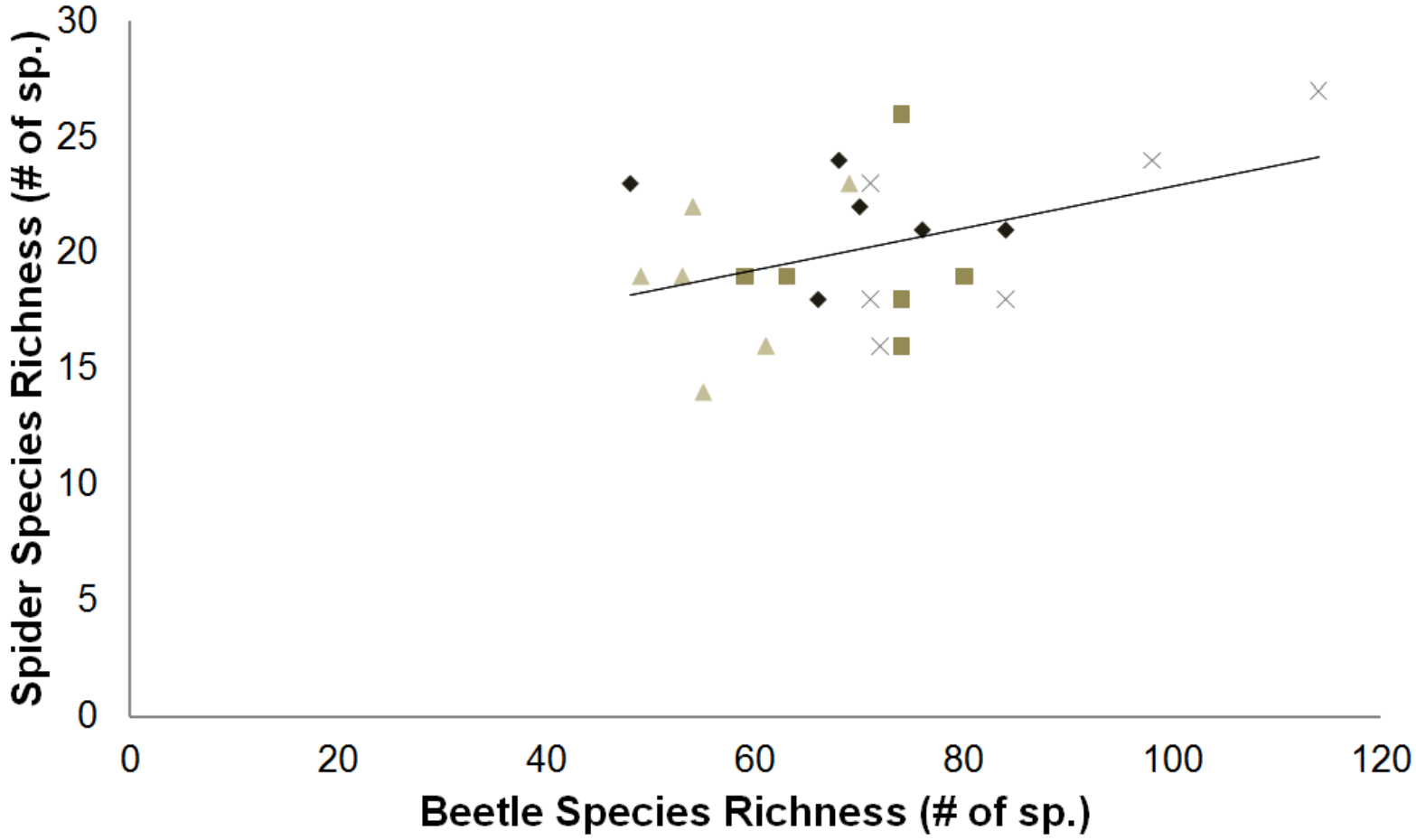

Figure 4. Correlation between spider and beetle species richness (R = 0.407, df = 22, P = 0.048). Symbols: ♦: thinned secondary growth, ■: old growth sites, ▲: un-thinned secondary growth, x: clearcuts.

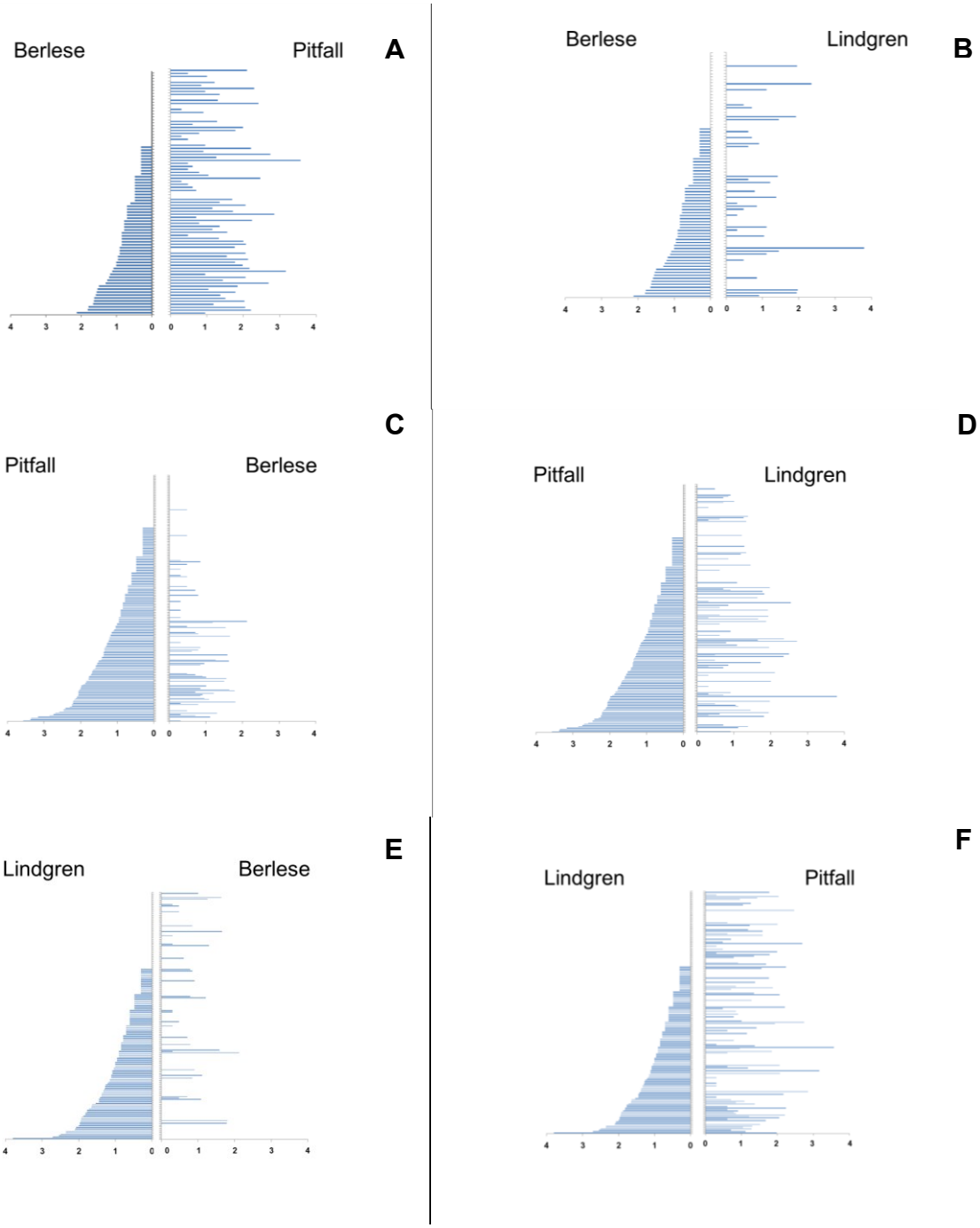

Figure 5. Collection methods compared using matched abundance plots. Rank-abundance (log scale) plot on the left of each graph for one trap method. The right half shows, for the same species, the abundance of those species from a different trap method. A: Berlese species vs. pitfall trap; B: Berlese species vs. Lindgren© funnel; C: Pitfall trap species vs. Berlese; D: Pitfall trap species vs. Lindgren©; E: Lindgren© funnel species vs. Berlese; F: Lindgren© funnel species vs. pitfall traps.

3.2 Taxonomic Assemblages:

3.2.1 Spiders: Non-metric Multi-Dimensional Scaling (NMDS) was used to assess the similarities of spider assemblages across treatments (Fig. 6A). Stress of the NMDS plot is a measure of how well dissimilarities between individual sites were preserved when these values were converted into distances on the two-dimensional plot (Clarke & Warrick, 2001). The spider NMDS had a stress of 0.17, which is a value that is within the range (0.01 – 0.19) that is useful for inference. Individual sites grouped separately within treatments with the possible exception of one old growth site. Circled groups on the NMDS plot are based on *a priori* groupings of treatments. NPMANOVA results indicated that almost all treatments were significantly different in their spider assemblages (Table 4). Old growth and un-thinned secondary growth were not significantly different because sites were closely grouped on the NMDS plot, indicating that these two treatments share many spider species.

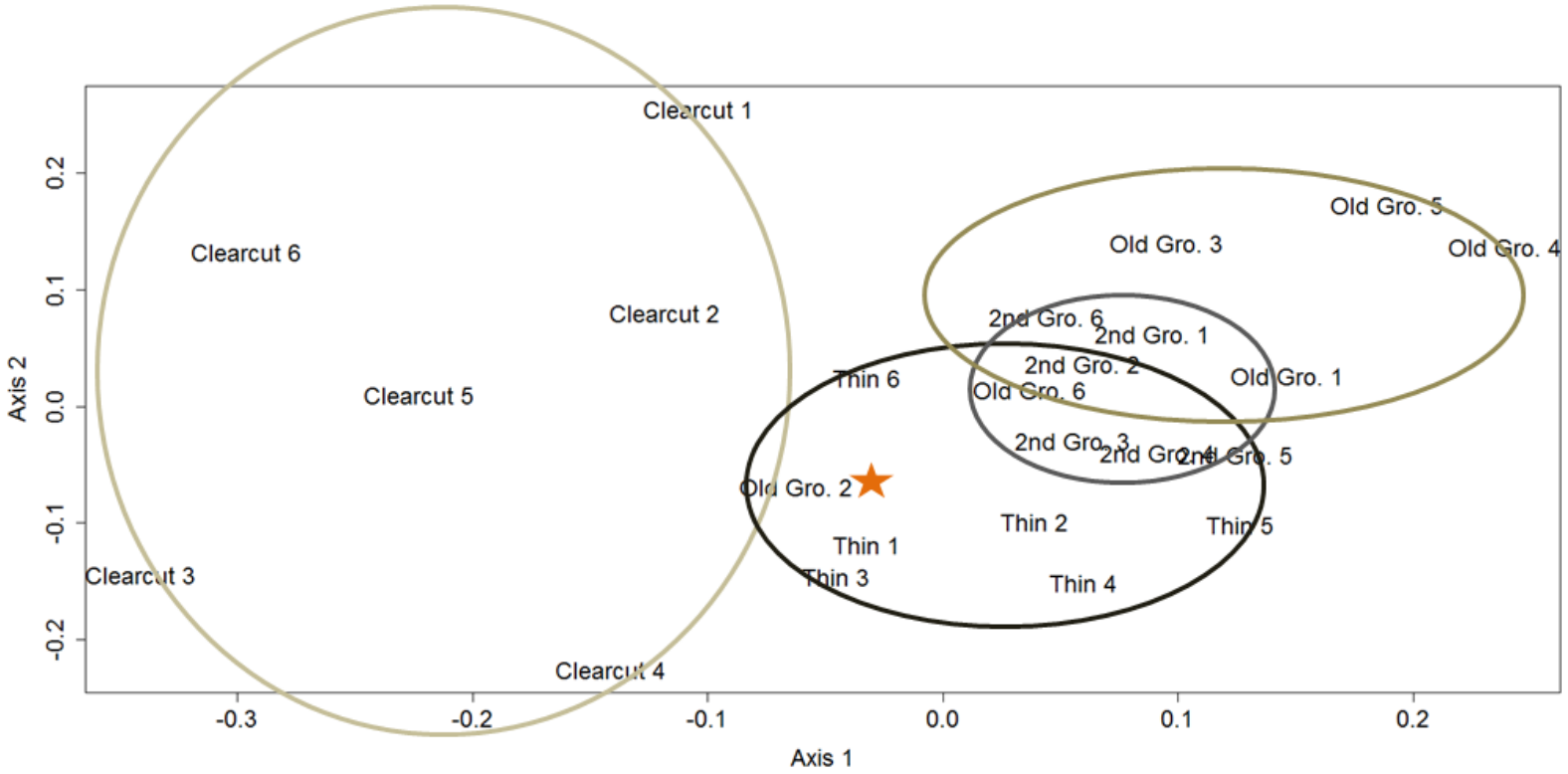

Figure 6A. Non-metric multidimensional scaling (NMDS) ordination of spider assemblages in thinned secondary growth (thins, black circle), old growth (gray-green circle), un-thinned secondary growth (2nd Gro, dark gray circle) and clearcuts (light gray circle). There are six replicates for each forest habitat (thins are pooled). Close proximity of sites indicates similarity, whereas a large distance between sites represents dissimilarity in spider assemblages. Ellipses represent groupings of sites with shared assemblage similarity. Stress level = 0.17. Star denotes a possible old growth site outlier.

Table 4. NPMANOVA results for comparisons between thinned secondary growth (Thins), old growth, secondary growth (2nd growth), and clearcuts. Spider and beetle assemblage distances calculated from the Bray-Curtis coefficient are the dependent variables. DF is degrees of freedom, F is the F-statistic, and P is the p-value.

	Spiders			Beetles		
Comparisons Between†:	DF	F	P	DF	F	P
Thins:						
Old growth	1	3.7207	0.008*	2	1.5343	0.012 ns
2nd growth	1	2.7471	0.001*	2	1.6767	0.019 ns
Clearcuts	1	3.2536	0.004*	2	1.4585	0.056 ns
Old growth:						
2nd growth	1	1.8808	0.038 ns	2	2.1858	0.003*
Clearcuts	1	3.7580	0.005*	2	2.4060	0.001*
2nd growth:						
Clearcuts	1	3.9402	0.005*	2	3.0364	0.001*

* P ≤ 0.008, ns non-significant (P>0.008). Alpha level with Bonferroni correction.
† Data from all treatments were log transformed to counter the weight influence of abundant species.

SIMPER was run between pairs of treatments to identify which species contributed to significant differences in spider assemblages. I focused mainly on differences or similarities found in assemblages between thinned secondary growth and the other treatments to understand how thinning secondary growth affects assemblages. In thinned secondary growth and old growth forest stands, 90% of the differences in spider assemblages were explained by variances in the abundance of 29 species (Table 5). There were 27 species accounting for 90% of the difference between thinned secondary growth and un-thinned secondary growth and 32 species accounting for 90% of the difference between thinned secondary growth and clearcuts (Table 6, Table 7). SIMPER results also showed that there was a total of 20 species highly associated (or found in higher abundances consistently) within specific treatments, which could be species to consider as ecological indicators: thinned secondary growth (7 species), old growth and un-thinned secondary growth (6 species), and clearcuts (7 species; Table 8). In particular, *Mythoplastoides erectus* and *Tapinocyba dietrichi* were species that were found only in old growth sites. Furthermore, *Lepthyphantes zibus* and *Symmigma minimum* were highly associated with old growth and un-thinned secondary growth forest stands, but were more abundant in thinned secondary growth when compared to clearcuts. In addition, *Sisicottus nesides* was highly associated with clearcut sites, but was more abundant in thinned secondary growth when compared to old growth and un-thinned secondary growth forest stands. These results indicate that thinned secondary growth treatments have some species that are characteristic of both old growth and clearcut habitats.

Table 5. SIMPER results characterizing differences in spider assemblages between thinned secondary growth and old growth. Species are ordered from highest to lowest contribution to total differences between treatments. Column headings: contr: average contribution from each species to the total dissimilarity between treatments; SD: standard deviation; ratio: ratio between contr and SD; av.a: average abundance of each species in thinned secondary growth; av.b: average abundance in each species in old growth; CSum: ordered cumulative contribution percentages to the total dissimilarity.

	Average Contributions to Total Dissimilarities					
Spider Species	contr	SD	Ratio	av.a	av.b	CSum
Ceratinops inflatus	0.03004	0.0179	1.68	1.500	2.840	0.076
Pocadicnemis pumila	0.02269	0.0140	1.62	1.356	0.557	0.133
Lepthyphantes zibus	0.02035	0.0126	1.62	0.305	1.175	0.185
Symmigma minimum	0.02000	0.0139	1.44	0.841	1.705	0.235
Agyneta perspicua	0.01915	0.0128	1.50	0.888	0.316	0.284
Walckenaeria occidentalis	0.01911	0.0150	1.27	0.906	0.955	0.332
Erigoninae sp.1 JS	0.01828	0.0091	2.00	0.069	0.892	0.378
Walckenaeria cornuella	0.01553	0.0097	1.60	1.184	1.071	0.417
Usofila pacifica	0.01520	0.0079	1.92	1.107	0.387	0.456
Ceratinella alaskae	0.01355	0.0120	1.13	0.329	0.485	0.490
Cicurina simplex	0.01339	0.0097	1.38	0.750	0.210	0.524
Centromerus nr.*longibulbus* Emerton	0.01200	0.0083	1.45	0.774	0.631	0.554
Robertus vigerens	0.01187	0.0087	1.37	0.617	0.275	0.584
Bathyphantes keenii	0.01068	0.0077	1.39	0.942	0.967	0.611
Cybaeus morosus	0.01044	0.0107	0.98	0.229	0.457	0.637
Bathyphantes orica	0.01023	0.0068	1.50	0.839	0.359	0.663
Sisicottus nesides	0.00959	0.0063	1.52	1.119	0.898	0.688
Cybaeus reticulatus	0.00952	0.0077	1.24	3.980	3.683	0.712
Oreonetides filicatus	0.00941	0.0072	1.31	0.263	0.424	0.735
Rugathodes sexpunctatus	0.00921	0.0080	1.16	1.987	1.959	0.759
Tapinocyba dietrichi	0.00867	0.0125	0.69	0.000	0.408	0.781
Dirksia cinctipes	0.00751	0.0062	1.22	0.188	0.363	0.800
Mythoplastoides erectus	0.00713	0.0105	0.68	0.000	0.329	0.818
Micrargus sp.1	0.00672	0.0046	1.45	0.296	0.126	0.835
Lepthyphantes zelatus	0.00668	0.0048	1.39	1.362	1.240	0.851
Usofila sp.	0.00615	0.0070	0.88	0.176	0.216	0.867
Agyneta protrudens	0.00519	0.0061	0.85	0.253	0.000	0.880
Erigoninae sp.5 JS	0.00508	0.0060	0.85	0.238	0.000	0.893
Microlinyphia dana	0.00447	0.0044	1.02	0.184	0.083	0.904

• All data are standardized due to uneven sampling in 2010 and log transformed to counter the weight of abundant species.

Table 6. SIMPER results characterizing differences in spider assemblages between un-thinned secondary growth and thinned secondary growth. Species are ordered from highest to lowest contribution to total differences between treatments. Column headings: contr: average contribution from each species to the total dissimilarity between treatments; SD: standard deviation; ratio: ratio between contr and SD; av.a: average abundance of each species in un-thinned secondary growth; av.b: average abundance in each species in thinned secondary growth; CSum: ordered cumulative contribution percentages to the total dissimilarity.

	Average Contributions to Total Dissimilarities					
Spider Species	contr	SD	ratio	av.a	av.b	CSum
Ceratinops inflatus	0.02699	0.0156	1.73	2.737	1.500	0.078
Pocadicnemis pumila	0.02389	0.0146	1.63	0.338	1.356	0.148
Walckenaeria occidentalis	0.01944	0.0170	1.14	0.697	0.906	0.204
Walckenaeria cornuella	0.01791	0.0135	1.33	1.877	1.184	0.256
Symmigma minimum	0.01790	0.0128	1.40	1.603	0.841	0.308
Agyneta perspicua	0.01746	0.0123	1.41	0.137	0.888	0.359
Rugathodes sexpunctatus	0.01480	0.0071	2.09	1.522	1.987	0.401
Lepthyphantes zelatus	0.01361	0.0093	1.47	1.968	1.362	0.441
Lepthyphantes zibus	0.01289	0.0101	1.28	0.713	0.305	0.478
Bathyphantes keenii	0.01267	0.0094	1.35	0.863	0.942	0.515
Cicurina simplex	0.01209	0.0087	1.39	0.729	0.750	0.550
Robertus vigerens	0.01125	0.0088	1.28	0.410	0.617	0.583
Cybaeus morosus	0.01059	0.0111	0.96	0.474	0.229	0.614
Usofila pacifica	0.01055	0.0071	1.50	0.974	1.107	0.644
Oreonetides filicatus	0.01027	0.0072	1.42	0.498	0.263	0.674
Sisicottus nesides	0.01021	0.0075	1.37	1.002	1.119	0.704
Centromerus nr.*longibulbus Emerton*	0.00928	0.0064	1.44	0.716	0.774	0.730
Cybaeus reticulatus	0.00843	0.0054	1.55	3.756	3.980	0.755
Bathyphantes orica	0.00815	0.0053	1.54	1.037	0.839	0.779
Ceratinella alaskae	0.00640	0.0145	0.44	0.000	0.329	0.797
Micrargus sp.1	0.00625	0.0045	1.38	0.000	0.296	0.815
Usofila sp.	0.00582	0.0054	1.08	0.211	0.176	0.832
Erigoninae sp.5 JS	0.00539	0.0053	1.02	0.120	0.238	0.848
Agyneta protrudens	0.00525	0.0062	0.85	0.000	0.253	0.863
Dirksia cinctipes	0.00512	0.0057	0.90	0.145	0.188	0.878
Walckenaeria directa	0.00440	0.0078	0.56	0.053	0.176	0.891
Microlinyphia dana	0.00413	0.0044	0.93	0.000	0.184	0.903

• All data are standardized due to uneven sampling in 2010 and log transformed to counter the weight of abundant species.

Table 7. SIMPER results characterizing differences in spider assemblages between thinned secondary growth and clearcuts. Species are ordered from highest to lowest contribution to total differences between treatments. Column headings: contr: average contribution from each species to the total dissimilarity between treatments; SD: standard deviation; ratio: ratio between contr and SD; av.a: average abundance of each species in thinned secondary growth; av.b: average abundance in each species in clearcuts; CSum: ordered cumulative contribution percentages to the total dissimilarity.

Average Contributions to Total Dissimilarities

Spider Species	contr	SD	ratio	av.a	av.b	CSum
Pardosa dorsuncata	0.0348	0.0234	1.49	0.199	1.868	0.077
Walckenaeria occidentalis	0.0257	0.0193	1.33	0.906	1.547	0.134
Pocadicnemis pumila	0.0214	0.0150	1.43	1.356	1.132	0.182
Rugathodes sexpunctatus	0.0214	0.0120	1.79	1.987	0.969	0.230
Agyneta perspicua	0.0183	0.0123	1.49	0.888	0.563	0.270
Sisicottus nesides	0.0181	0.0102	1.78	1.119	1.796	0.311
Cybaeus morosus	0.0179	0.0169	1.06	0.229	0.918	0.350
Symmigma minimum	0.0167	0.0093	1.79	0.841	0.451	0.388
Walckenaeria cornuella	0.0166	0.0116	1.43	1.184	1.172	0.424
Usofila pacifica	0.0163	0.0080	2.03	1.107	0.362	0.461
Cicurina simplex	0.0145	0.0106	1.37	0.750	0.158	0.493
Centromerus nr.*longibulbus* Emerton	0.0145	0.0077	1.88	0.774	0.097	0.525
Ceratinops inflatus	0.0142	0.0099	1.43	1.500	1.809	0.557
Bathyphantes keenii	0.0136	0.0092	1.48	0.942	0.727	0.587
Clubiona pacifica	0.0126	0.0093	1.36	0.000	0.636	0.615
Bathyphantes orica	0.0119	0.0062	1.92	0.839	0.516	0.641
Robertus vigerens	0.0112	0.0069	1.62	0.617	0.805	0.666
Cybaeus reticulatus	0.0107	0.0086	1.23	3.980	3.622	0.690
Ceratinella acerea	0.0104	0.0153	0.68	0.000	0.546	0.713
Oreonetides filicatus	0.0101	0.0073	1.38	0.263	0.497	0.735
Ceratinella alaskae	0.0100	0.0133	0.75	0.329	0.285	0.758
Lepthyphantes zelatus	0.0074	0.0057	1.30	1.362	1.283	0.774
Agyneta protrudens	0.0071	0.0067	1.06	0.253	0.260	0.790
Microlinyphia dana	0.0069	0.0052	1.34	0.184	0.389	0.805
Cryphoeca exlineae	0.0060	0.0046	1.31	0.000	0.295	0.819
Micrargus sp.1	0.0060	0.0044	1.36	0.296	0.097	0.832
Xysticus pretiosus	0.0059	0.0073	0.81	0.077	0.254	0.845
Dirksia cinctipes	0.0059	0.0066	0.89	0.188	0.205	0.858
Walckenaeria directa	0.0056	0.0090	0.62	0.176	0.144	0.871
Lepthyphantes zibus	0.0051	0.0034	1.49	0.305	0.120	0.882
Erigoninae sp.5 JS	0.0049	0.0058	0.85	0.238	0.000	0.893
Usofila sp.	0.0044	0.0059	0.75	0.176	0.097	0.903

• All data are standardized and transformed to counter abundant species

Table 8. Spider species and total number of individuals highly associated with treatments: thinned secondary growth (Thins), old growth (OG), un-thinned secondary growth (2nd growth), and clearcuts.

Species	Thins	Old growth	2nd growth	Clearcuts
Highly Associated with Thins:				
Micrargus sp. 1	6	2	0	1
Agyneta perspicua	25	10	3	14
Centromerus nr. *longibulbus*	20	13	13	1
Cicurina simplex	21	3	14	2
Cybaeus reticulatus	940	434	540	347
Rugathodes sexpunctatus	105	73	49	16
Usofila pacifica	35	5	23	6
Highly Associated with OG and 2nd growth:				
Ceratinops inflatus	63	193	206	55
Lepthyphantes zibus‡	6	29	20	2
Symmigma minimum‡	25	54	63	10
Erigoninae sp. 1	1	16	1	2
Mythoplastoides erectus *	0	6	0	0
Tapinocyba dietrichi *	0	7	0	0
Highly Associated with Clearcuts:				
Ceratinella acerea	0	3	1	13
Clubiona pacifica	0	0	2	8
Cryphoeca exlineae	0	1	1	4
Pardosa dorsuncata	4	0	0	154
Xysticus pretiosus	1	0	0	4
Cybaeus morosus	5	8	13	19
Sisicottus nesides⁑	32	17	25	46

• Old growth and un-thinned secondary growth grouped together for common species due to no significant difference in spider assemblages
‡ Associated with thinned secondary growth when compared to clearcuts
* Highly associated with old growth only
⁑ Associated with thinned secondary growth when compared to old growth and un-thinned secondary growth

3.2.2 Beetles: In contrast to spiders, beetle assemblages showed only two distinct groupings, one for old growth and one for un-thinned secondary growth habitats (Fig. 6B). Thinned secondary growth sites had highly variable beetle assemblages resulting in four different groupings on the NMDS plot. This variability was not related to different thinning treatment levels of secondary growth. Clearcut sites formed two different groups, which correspond with clearcut sites 1 and 2 being fresh clearcut sites, while the other clearcuts sites are a few years older (4-5 years). The stress level for the NMDS plot was 0.16, indicating that the NMDS plot results are within the range that is useful for inference. NPMANOVA showed significant differences in beetle assemblages between old growth, un-thinned secondary growth, and clearcuts (Table 4). Thinned secondary growth was not significantly different from any treatment due to the high variability in beetle assemblages.

Although there were no significant differences between thinned secondary growth and any other treatment, I examined whether species were highly associated with old growth, un-thinned secondary growth, or clearcuts. There were 65 total species that were highly associated among the treatments: old growth (22 species), un-thinned secondary growth (15 species), and clearcuts (28 species) (Table 9). *Phlaeopterus lagrandeuri* was unique to old growth sites while *Atomaria* nr. *ornata* and *Pterostichus adstrictus* occurred only in clearcut sites. Individual sites of thinned secondary growth forest stands tended to have variable combinations of species commonly found in old growth, un-thinned secondary growth, and clearcut sites (not shown).

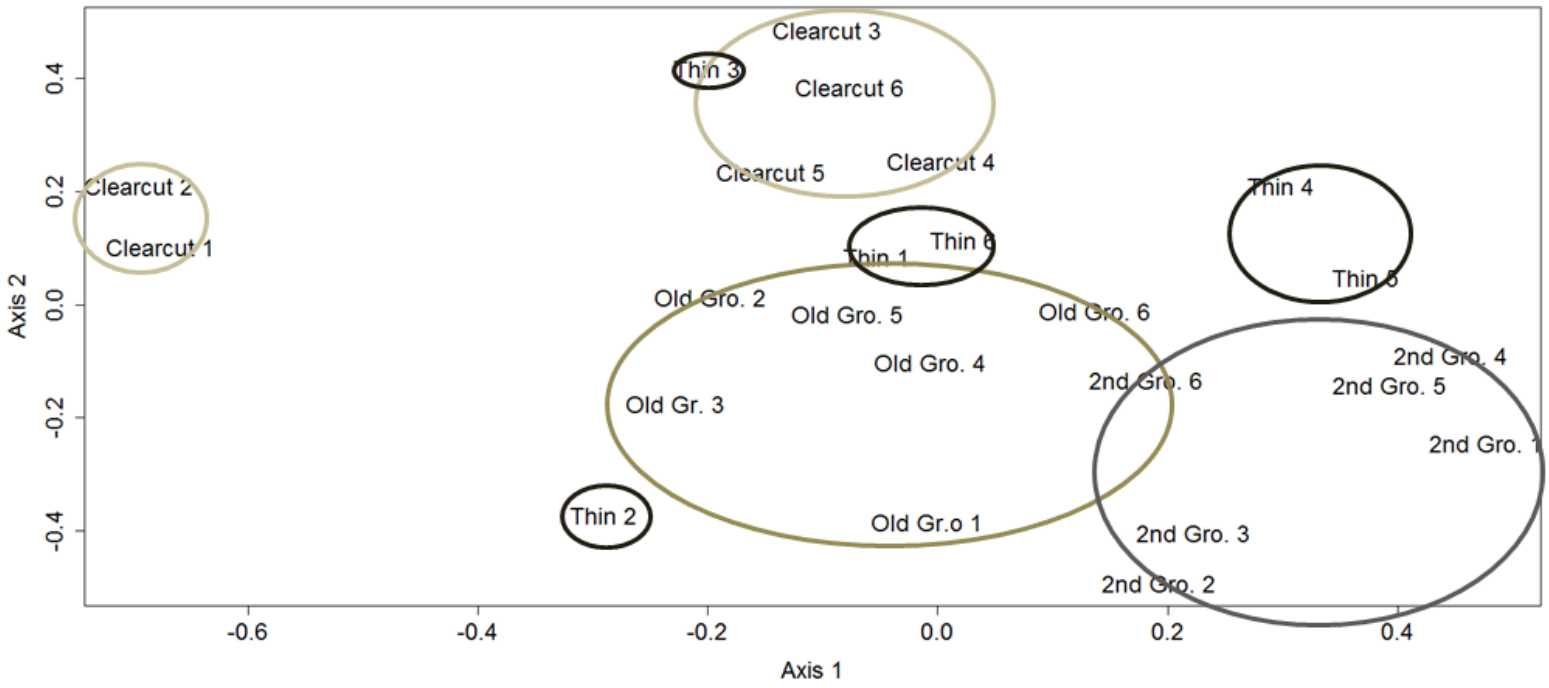

Figure 6B. Non-metric multidimensional scaling (NMDS) ordination of beetle assemblages in thinned secondary growth (thins, black circle), old growth (gray-green circle), un-thinned secondary growth (2nd Gro, dark gray circle) and clearcuts (light gray circle). There are six replicates for each forest habitat (thins are pooled). Close proximity of sites indicates similarity, whereas a large distance between sites represents dissimilarity in spider assemblages. Ellipses represent groupings of sites with shared assemblage similarity. Stress level = 0.16.

Table 9. Beetle species and total number of individuals highly associated with treatments: old growth, un-thinned secondary growth (2nd growth), and clearcuts. Thinned secondary growth was not significantly different from any other treatment in beetle assemblage

Species	Thins	Old growth	2nd growth	Clearcuts
Highly Associated with Old growth:				
Autalia truncatula	7	14	1	5
Cephaloon bicolor	8	9	0	5
Dictyoptera aurora	26	16	4	2
Eusphalerum sp.5	1	5	0	3
Evodinus vancouveri	6	5	0	3
Foveoscapha terracola	0	5	2	1
Nicrophorus defodiens	3	14	1	0
Peltastica tuberculata	3	8	1	2
*Phlaeopterus lagrandeuri**	0	5	0	0
Pinodytes cryptophagoides	0	8	2	0
Quedius plagiatus	2	9	3	0
Rhizophagus sculpturatus	2	17	2	2
Tachinus semirufus	0	7	2	2
Atomaria nr. *affinis*	0	8	2	1
Agoliinus piceatus	3	6	4	4
Atrecus macrocephalus	18	32	17	23
Dictyoptera simplicipes	68	37	28	29
Ochthephilus biimpressus	9	41	11	13
Rhinosimus viridiaeneus	7	87	27	3
Rhizophagus dimidiatus	14	74	15	13
Scaphinotus angusticollis	628	1485	1306	336
Scaphinotus marginatus	281	167	45	41
Cryptophagus sp.	22	46	9	24
Lioligus nitidus	10	16	0	9

Table 9. Continued

Species	Thins	Old growth	2nd growth	Clearcuts
Highly Associated with 2nd growth:				
Caelius browni	0	0	9	1
Orchesia sp.	3	0	8	0
Scydmaeninae sp.25	1	5	6	3
Sonoma parviceps	5	3	9	2
Staphylinidae sp.15.1	6	1	16	0
Agathidium sp.1	34	22	46	43
Lederia arctica	16	5	29	18
Bolitobius cingulatus	18	10	65	7
Catops sp.	60	69	76	33
Henotiderus n.sp.	39	20	71	9
Hylurgops rugipennis	64	16	150	11
Lordithon thoracicus	3	12	15	0
Pterostichus amethystinus	72	34	107	50
Scydmaeninae sp.13	17	28	73	17
Sonoma sp.	42	62	85	55
Highly Associated with Clearcuts:				
Agabus sp.1	3	3	2	15
Ampedus carbonicolor	10	2	3	55
Atomaria nr. *ornata*†	0	0	0	12
Ciidae sp.1	5	3	0	9
Dichelotarsus sp.	7	2	1	13
Ditylus gracilis	7	3	4	26
Dolurgus pumilus	6	1	0	27
Oxytelus laqueatus	3	2	1	21
Pelecomalium sp.	4	1	1	15
Phellopsis porcata	1	1	2	12
Pterostichus adstrictus†	0	0	0	9

Table 9. Continued

Species	Thins	Old growth	2nd growth	Clearcuts
Highly Associated with Clearcuts cont.				
Rhagium inquisitor	1	0	0	18
Agathidium sp.2	14	7	35	71
Agathidium sp.7	15	0	11	23
Athous rufiventris	22	7	9	24
Anaspis sp.1	115	80	5	167
Cucujus clavipes	1	15	6	37
Cychrus tuberculatus	96	87	52	148
Epuraea sp.1	69	94	23	144
Epuraea sp.2	7	7	0	11
Epuraea sp.3	4	8	0	16
Eusphalerum sp.1	1564	1336	172	3391
Liotrichus umbricolus	25	11	4	52
Liotrichus volitans	11	9	5	31
Listemus acuminatus	31	6	2	61
Notiophilus sylvaticus	2	13	2	92
Ptiliidae sp.1	83	74	11	144
Rhyncolus brunneus	21	14	9	32

* Highly associated with old growth only
†Highly associated with clearcuts only

3.3 Feeding Groups:

For both beetles and spiders, there were no differences in the relative abundance of different feeding groups among treatments in NMDS plots, which was confirmed by NPMANOVA.

3.4 Vegetation Correlations:

Vegetation surveys showed that overall old growth sites had taller trees with a greater DBH than other treatments (Table 10; no statistical tests performed). Old growth and un-thinned secondary growth sites also had larger LAI and BA values than other treatments. Thinned secondary growth and clearcut sites had higher percent cover of understory vegetation than old growth or un-thinned secondary growth sites. Correlations were used to see whether differences in spider and beetle assemblages reflected the vegetation characteristics found within each treatment.

3.4.1 Spiders: Vegetation variable overlays and correlations to NMDS axes indicate that all vegetation variables measured were correlated (Spearman's rho) to spider biotic structure (Fig. 7A). Positive or negative correlations do not show biological significance and are related to the NMDS axes. The strongest relationships were found between NMDS axes (spider assemblages) and LAI (rho = 0.699) and percent of understory vegetation cover (rho = -0.678). Slightly weaker positive relationships were found between NMDS axes and the height of trees (rho = 0.545), BA (rho = 0.507), and DBH (rho = 0.436). These correlations indicate that compositions of spider assemblages were mainly influenced by the amount of sunlight penetrating through the canopy and percent of understory vegetation cover.

Table 10. Summary values for vegetation surveys in thinned secondary growth (Thins), old growth, un-thinned secondary growth (2nd growth), and clearcuts.

	Forest Treatments			
Vegetation Variables:	Thins	Old Growth	2nd growth	Clearcut
Tree Height (m)	8.68	42.37	6.54	4.63
Diameter at Breast Height (DBH) (cm)	15.86	56.78	10.36	6.81
Basal Area (BA) (m^2/ha)	11.64	48.88	41.68	1.02
Leaf Area Index (LAI)	1.27	3.24	4.29	0.41
Percent Cover of Understory (m)	0.40	0.10	0.17	0.25

- Tree height, DBH, and BA represent the mean of all tree species.
- Percent Cover of Understory is based on the cover of all plants excluding trees

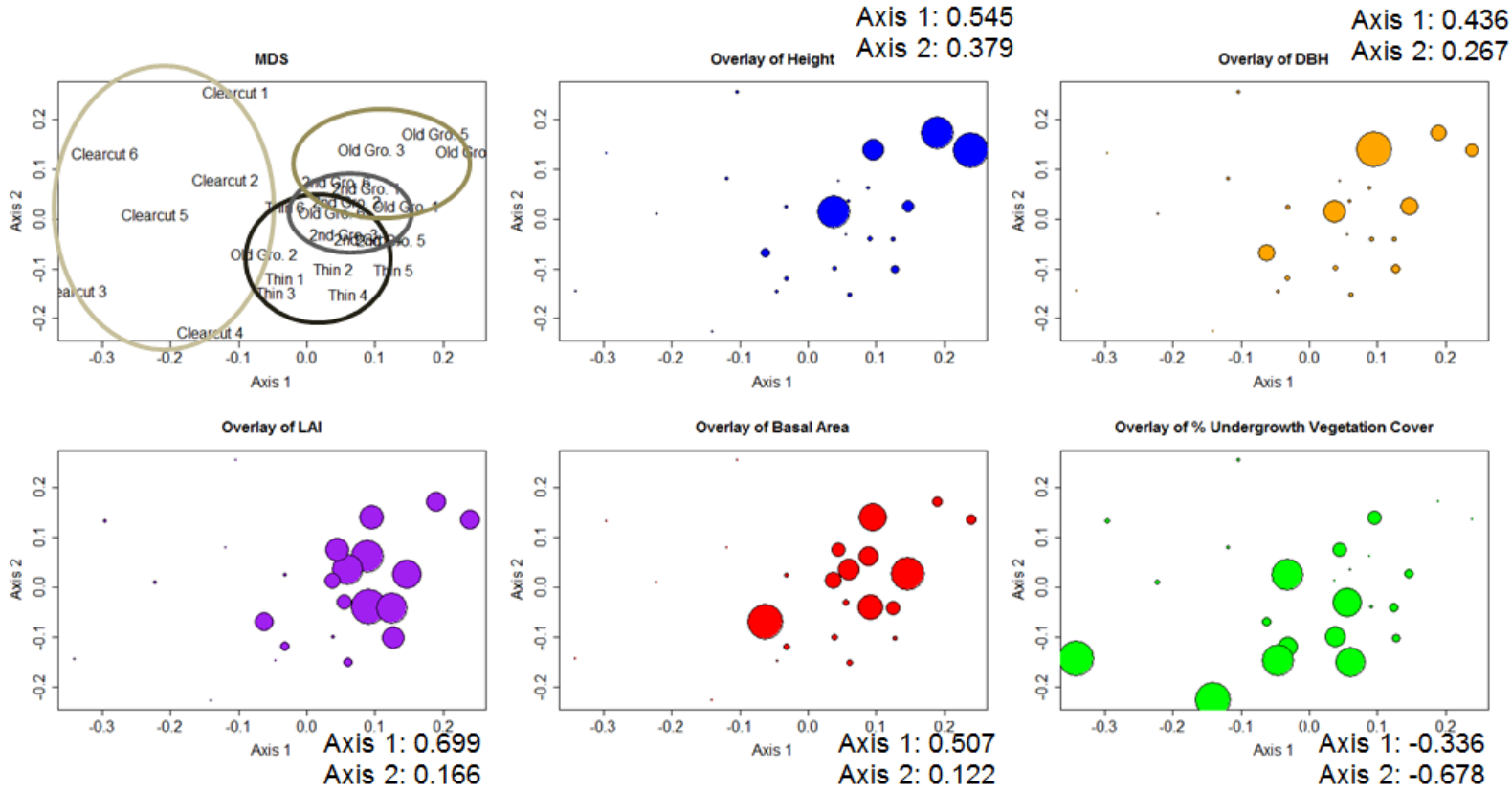

Fig. 7A. Overlay of vegetation variables (tree height, diameter at breast height (DBH), leaf area index (LAI), basal area (BA) and % of undergrowth vegetation cover) on NMDS ordination of spider assemblages. Larger circles denote higher variable values and smaller circles indicate lower variable values. Vegetation correlations to NMDS axes located above each vegetation variable.

BIOENV was also used to look for the maximum correlations between combinations of vegetation variables and spider biotic structure. Height of trees, LAI, and percent cover of understory vegetation had the highest correlation to spider assemblages (0.327) (Table 11). However, this correlation is only moderately strong.

3.4.2 Beetles: Vegetation overlays and correlations (Spearman's rho) to NMDS axes show that only two vegetation variables were strongly correlated with beetle biotic structure (Fig. 7B). LAI (rho = -0.819) and BA (rho = -0.491) had the strongest correlations with NMDS axes and beetle assemblages. Height of trees, DBH, and percent cover of undergrowth plants were not highly correlated to beetle assemblage structure.

BIOENV results indicated that only one vegetation variable was highly correlated with beetle biotic structure (Table 12). LAI had the highest correlation (0.468) followed by the combination of LAI and percent understory cover (0.397). All other combinations of vegetation variables had fairly low correlations to beetle community structure.

3.4.3 Spiders and Beetles: LAI, which is inversely related to the amount of sunlight that can penetrate through the canopy, had the strongest influence on the composition of both spider and beetle assemblages.

Table 11. BIOENV results for correlation of multiple combinations of vegetation variables to spider biotic structure. Highest correlations for single, double, triple, quadruple, and quintuple combinations of vegetation variables shown. * highest correlation.

Vegetation Variables)	Size	Correlation
LAI	1	0.1770
LAI Cover	2	0.3180
Height LAI Cover	3	0.3265*
Height LAI BA Cover	4	0.3178
Height DBH LAI BA Cover	5	0.2383

- LAI: Leaf area index
- Cover: % Understory cover for vascular plants
- Height: Height of trees
- BA: Basal area
- DBH: Diameter at breast height

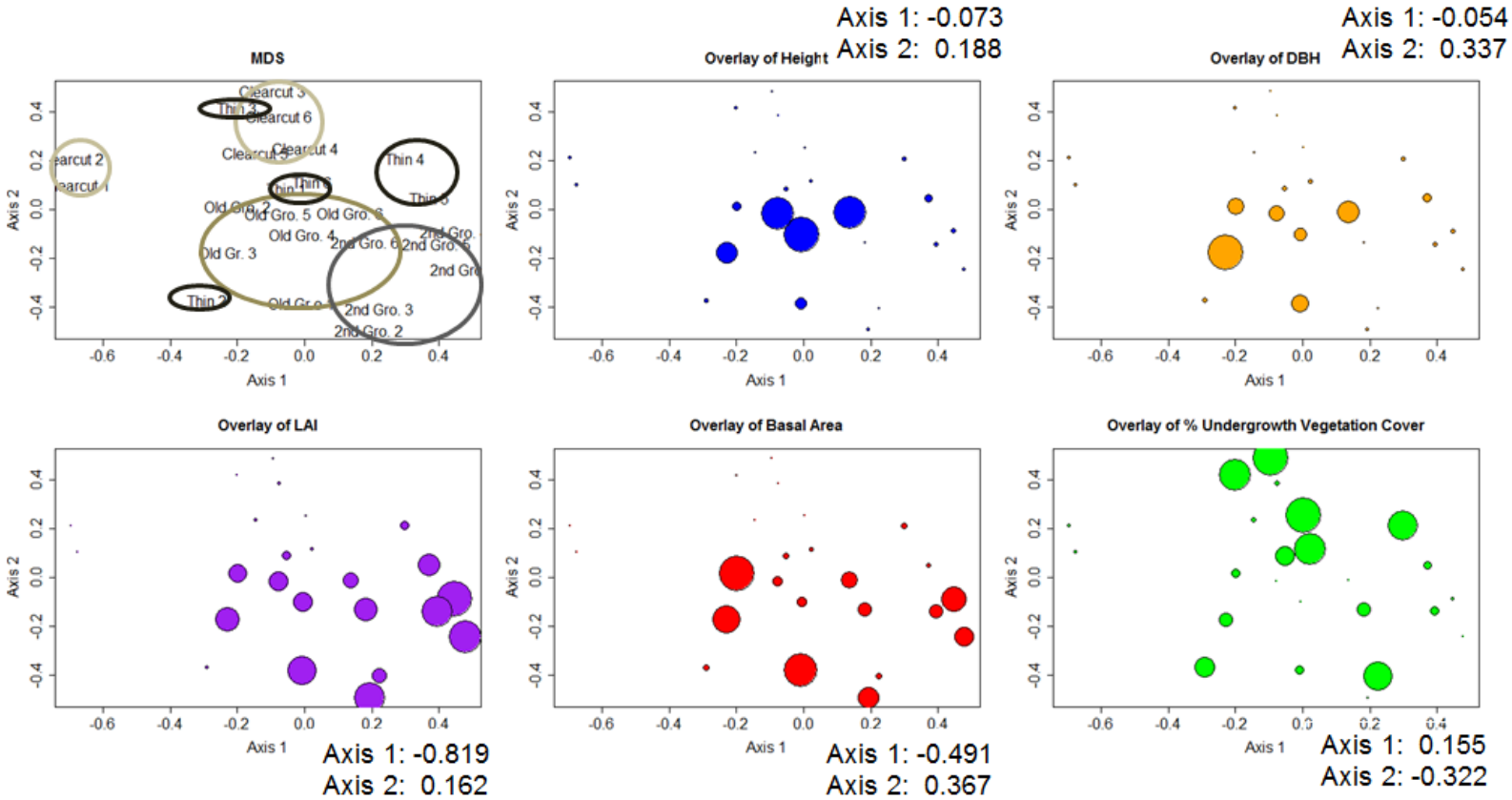

Figure 7B. Overlay of vegetation variables (tree height, diameter at breast height (DBH), leaf area index (LAI), basal area (BA) and % of undergrowth vegetation cover) on NMDS ordination of beetle assemblages. Larger circles denote higher variable values and smaller circles indicate lower variable values. Vegetation correlations to NMDS axes located above each vegetation variable.

Table 12. BIOENV results for correlation of multiple combinations of vegetation variables to beetle biotic structure. Highest correlations for single, double, triple, quadruple, and quintuple combinations of vegetation variables shown. * highest correlation.

Vegetation Variables)	Size	Correlation
LAI	1	0.4681*
LAI Cover	2	0.3966
LAI BA Cover	3	0.3678
DBH LAI BA Cover	4	0.3306
Height DBH LAI BA Cover	5	0.2496

- LAI: Leaf area index
- Cover: % Understory cover for vascular plants
- Height: Height of trees
- BA: Basal area
- DBH: Diameter at breast height

Chapter 4 Discussion

4.1 Overview:

To understand how the practice of thinning young even-aged forest stands affects forest biodiversity, I compared spider and beetle species richness, diversity, and assemblages of thinned secondary growth to old growth, un-thinned secondary growth, and clearcuts. Within spider and beetle populations, I looked for ecological indicators in each treatment. No significant differences were found in species richness or diversity between thinned secondary growth and the other treatments; therefore, the thinning of secondary growth did not impact species richness or diversity of spiders and beetles. Analysis of spider and beetle assemblages indicated that spider composition in thinned secondary growth was significantly different from the other treatments, whereas beetle composition in thinned secondary growth was not different from other treatments. Particular species that were identified as being highly associated with treatments were categorized as potential ecological indicators of recovering forests.

4.2 Species Richness and Diversity:

My results for species richness and diversity contrast with those of several previous studies with whether or not significant differences were found between different forest treatments (Franc & Götmark, 2008; Heliölä, Koivula, & Niemelä, 2001; Klimaszewski et al., 2008; Pohl, Langor, & Spence, 2007; Pohl et al., 2008). I found no significant differences in spider species richness or diversity between treatments, while beetle species richness was high in clearcuts, although this result was not significantly different from thinned secondary growth or old growth forest stands. A few studies

found similar results to my study with no significant differences found for effects of different forestry practices on species richness and diversity of ground beetles (e.g. Atelgrim, Sjoberg, & Ball, 1997; Sustek, 1981). Conversely, numerous studies have found significant differences in species richness and diversity between different forest treatments such as significantly higher species richness and diversity of spiders and beetles in clearcuts compared to other forest management types (e.g. Franc & Götmark, 2008; Heliölä et al., 2001; Klimaszewski et al., 2008; Pohl et al., 2007, 2008). Explanations for high species richness and diversity during the first few years after clearcutting are based on the invasion of open habitat specialists into clearcut areas while a few forest specialists persist (Niemelä et al., 1993; Pohl et al., 2008). Contrasting results indicate that there may be several factors affecting how species richness and diversity respond to different forest treatments.

Differences between my results and previous published findings may be partly due to differences in methodology. Studies differ in geographic and environmental variation, the season the study was conducted, types of harvest treatments, the number or replicates per treatment, and the species studied, and these factors can affect species richness and diversity results (Atelgrim et al., 1997; Pajunen, Haila, Halme, Niemelä, & Punttila, 1995; Pohl et al., 2008). For example, most previous studies have only used one group of arthropods (i.e. Carabidae, Staphylinidae, or ground dwelling spiders) to compare forest management practices, and most have used only one collection method (i.e. pitfall traps) to collect specimens. Pitfall traps have been criticized for measuring activity of individuals rather than species presence, creating a bias towards collecting more individuals and species in hot dry environments

(Melbourne, 1999). Most studies also had small sample sizes ranging from 10 -15 pitfall traps per site (varying between 9 – 23 plotted sites) with only 5 -19 trapping days total (Atelgrim et al., 1997; Pajunen et al., 1995). In contrast, my study included all species of spiders and beetles and used three different trapping methods, collecting as many possible functional groups. I also had larger sample sizes to increase statistical power by collecting from seven traps from each of the 24 sites for a total of 84 trapping days in two field seasons. In addition, most of my study sites were plots created by the TWYGS program, which is a management effort that was highly replicated and wide spread throughout Southeast Alaska. Therefore, my study is exceptionally comprehensive and the data allows for concrete conclusions about how species richness and diversity respond to forest management in coastal temperate rain forests.

4.3 Assemblages:

Spider and beetle assemblages differed between some treatments and were associated with some vegetation variables. Previous studies have also shown differences in arthropod assemblages between different forestry practices (Buddle, Spence, & Langor, 2000; Franc & Götmark, 2008; Klimaszewski et al., 2008; Niemelä et al., 1988, 1993; Pajunen et al., 1995; Pohl et al., 2007, 2008). For example, Franc and Götmark (2008) found significant differences in assemblages of saproxylic and herbivorous beetles when comparing unmanaged to partially-cut forest stands. In my study, I found significant differences in spider assemblages between all treatments save two, while beetle assemblages were found to be significantly different between old growth, un-thinned secondary growth, and clearcuts. Surprisingly, spider assemblages of un-thinned secondary growth were not significantly different from old growth

assemblages. In addition, even though beetle assemblages were different between the un-thinned secondary growth and old growth stands, the group of un-thinned secondary growth sites was close in assemblage structure to the group of old growth sites on the NMDS plot. A possible explanation for this outcome would be that LAI was the vegetation variable with the highest influence on spider and beetle assemblage. Both old growth and un-thinned secondary growth forest stands had high LAI values, resulting in dark, cool, moist habitats. This is in stark contrast to clearcuts which have low LAI values, creating bright, hot, dry environments.

Differences between spider and beetle assemblages were also shown within thinned secondary growth treatments compared to other treatments. Thinned secondary growth sites grouped together on the NMDS plot for spider assemblages and were significantly different from other treatments. However, beetle assemblages for thinned secondary growth sites resulted in four different groupings that were not significantly different from the other treatments. A plausible cause for this difference is that beetles have high species richness compared to spiders. In Alaska, ~ 1,448 beetle species have been documented (Bousquet, Bouchard, Davies, & Sikes, 2013) and 212 species were collected on POW alone in this study. In contrast, only ~ 382 spider species have been documented in Alaska (Paquin, Buckle, Dupérré, & Dondale, 2010), with 59 species collected in the study area. An updated count for spider species in Alaska that includes unpublished records is ~ 599 species (Arctos, 2014). Therefore, Alaska has approximately two to four times more beetle species than spider species. Consequently, high beetle species richness and diversity may play a role in the variability of how species assemblages form in new habitats through the lottery model.

In the lottery model, space is a limiting resource and vacant space is recolonized by the first few species to arrive on site (Munday, 2004). The first few species to arrive can shape the species assemblage through interactions with other species that come to the new habitat. Therefore, beetle assemblages may be more variable than spider assemblages, because the high species richness of beetles can cause there to be many different species that could arrive first at the thinned secondary growth sites.

Spider and beetle assemblages in thinned secondary growth are not completely recovered to an old growth forest state. Spider and beetle assemblages within thinned secondary growth were not closer in structure to old growth assemblages than to those of other treatments. In addition, un-thinned secondary growth had spider and beetle assemblages that were close in structure to old growth assemblages. This result does not support my hypothesis that thinned secondary growth would be closer in assemblage structure to old growth than un-thinned secondary growth. However, thinned treatments were only applied a relatively short time ago (2002-2006) compared to the time of this study; therefore, assemblages will continue to change in thinned secondary growth. Hanley et al. (2013) confirms that the short time that has elapsed since post treatment are only preliminary results and subsequent measurements are needed over time to evaluate the effects of thinning treatments on vegetation and forest biota. Over time, thinned secondary growth will likely develop old growth characteristics such as increased LAI. In addition, gaps in the thinned secondary growth canopy will allow younger generation trees to grow, creating an uneven canopy and allowing an amount of sunlight comparable to old growth stands to penetrate to the forest floor. In contrast, un-thinned secondary growth will continue to have an even canopy, not

allowing sunlight to pass through to the forest floor. Therefore, a hypothesis for future work would be to test if thinned secondary growth resembles old growth more than un-thinned secondary growth assemblages as time passes.

4.4 Ecological Indicators:

Abundant open habitat specialists (OHS), forest specialists (FS) and thinned secondary growth associated species were identified as potential ecological indicators. High numbers of FS found within thinned treatments would indicate later stages of forest recovery, while high numbers of OHS would indicate that thinned treatments may be far from forest recovery or in the early stages of forest recovery. For spiders, *Cybaeus reticulatus* (Cybaeidae), *Ceratinops inflatus* (Linyphiidae), and *Pardosa dorsuncata* (Lycosidae) were all collected in high numbers in thinned secondary growth, old growth and un-thinned secondary growth, and clearcuts respectively. *Cybaeus reticulatus* are active predators that are commonly found on moist forest floors under debris or leaf litter (Bradley, 2013). Thinned secondary growth has both moist forest floors and an abundance of tree debris left from thinning, creating an ideal habitat for *C.* reticulatus. Therefore, *C. reticulatus* was highly associated with thinned secondary growth. *Ceratinops inflatus* (Linyphiidae) are web builders that are frequently found in high numbers on forest floors (Buddle et al., 2000; Huber, 2007; Matveinen-Huju & Koivula, 2008; Pajunen et al., 1995) and were identified as FS. *Pardosa dorsuncata* are active sun-loving predators (Levi & Levi, 1990) and were categorized as OHS. For beetles, *Scaphinotus angusticollis* (Carabidae) and *Eusphalerum* sp. (Staphylinidae) were collected in high numbers within old growth and clearcuts respectively. *Scaphinotus angusticollis* inhabit cool damp forests and are molluscivorous with

mouthparts adapted to eat snails (Arnett & Thomas, 2001). Previous studies have also found the genus *Scaphinotus* in higher numbers within forests and lower numbers within clearcut habitats (Heliölä et al., 2001; Lenski, 1982). *Eusphalerum* species are pollen feeders in flowers from shrubs, herbs, and trees (Arnett & Thomas, 2001). Clearcuts had high percent cover of understory vegetation that may provide more pollen than other forest habitats, resulting in collecting high numbers of *Eusphalerum* species.

Some species identified as ecological indicators were abundant across all treatments. Although these species may be considered generalists, they were found to be numerically more abundant in specific treatments. For example, *C. reticulatus* was collected in numbers ranging from 347 – 940 specimens per treatment; however, thinned secondary growth had ~ 2 – 3 times more *C. reticulatus* compared to other treatments. *Scaphinotus angusticollis* was also collected in high numbers across habitats ranging from 336 – 1485 specimens per treatment, but were ~ 2 – 4.5 times more numerous in old growth compared to clearcuts and thinned secondary growth respectively. Although there are not specific rules about how to select effective ecological indicators (Langor & Spence, 2006), species that show a strong relationship with the disturbance factor of interest, such as one specific treatment having more than double the number of specimens found in a different treatment, can be used as effective ecological indicators.

Thinned secondary growth forest stands may be in the process of recovering to an old growth forest state. Old growth forests had high densities of FS and clearcuts had a high abundance of OHS, whereas thinned and un-thinned secondary growth had a mix of OHS and FS. This result supports my hypothesis that thinned secondary

growth would have a combination of both FS and OHS. Past studies have shown comparable results with OHS increasing in abundance while FS decline with clearcutting, followed by an increase in FS and a decrease in OHS as the forest regenerates and the forest canopy closes (Buddle et al., 2000; Koivula, Kukkonen, & Niemelä, 2002; Matveinen-Huju & Koivula, 2008; Niemelä et al., 1988, 1993; Pajunen et al., 1995; Pohl et al., 2007, 2008; Spence, Langor, Niemelä, Cárcamo, & Currie, 1996; Willett, 2001). For example, Pohl et al. (2008) found both OHS and FS in mid-successional regenerating forests. In my study, a combination of OHS and FS within thinned secondary growth of may be a result of this treatment having both open and shaded tree areas, providing habitat for FS and OHS. In addition, some spider species have been found to be characteristic of young regenerating stands (Pohl et al., 2008). In my study, I found that specific spider species were highly associated with thinned secondary growth stands. Huhta (1965) and Schowalter et al. (2003) found similar results showing specific spider species that were found in higher abundances within thinned secondary growth. Overall, thinned secondary growth at the time of my study has shown to be a habitat for both OHS and FS. If thinned secondary growth forest is recovering to an old growth environment, then OHS should start to decline and FS increase in numbers as the canopy closes over time.

Chapter 5 Conclusions:

Commercial logging and the resulting dense young even-aged stands can cause the decline of old growth forest specialists across a landscape. However, logging on POW did not significantly negatively impact spider and beetle biodiversity, though there were changes in assemblages. Dense un-thinned young even-aged stands, did have somewhat lower spider and beetle diversity relative to other treatments, and therefore, thinning young even-aged stands may help to maintain forest biodiversity and hasten the recovery process to an old growth forest state. To date, the TWYGS program is the most extensive and highly replicated management effort of young even-aged forest stands conducted in Southeast Alaska (Hanley et al., 2013). Therefore, strong conclusions can be made about how thinned secondary growth affects forest biota. However, questions remain regarding how spider and beetle assemblages will change within thinned secondary growth forest stands and whether OHS will decline and FS will increase in numbers over time. Continuing evaluations of how thinned secondary growth affects forest biota are needed as these treatments mature and LAI increases with closing canopy.

In summary, my first hypothesis was supported showing that thinned secondary growth had a mix of FS and OHS, whereas my second hypothesis that thinned secondary growth would be further in the process of recovery than un-thinned secondary growth was not supported. However, thinned secondary growth did not negatively affect spider or beetle species richness and diversity relative to unthinned secondary growth and old growth treatments. In fact, most old growth specialists were found within thinned secondary growth (as well as un-thinned secondary growth),

showing that thinning treatments provide a habitat for FS to survive. Future monitoring is necessary to evaluate thinned secondary growth in comparison to un-thinned secondary growth assemblages. Nevertheless, the management technique of thinning secondary growth forest stands, may successfully hasten the maturation of young even-aged stands by increasing the productivity of individual trees (Hanley et al., 2013). An additional recommendation for future forest management would be to leave substantial areas of old growth forest next to clearcut sites. This would not only provide an area for old growth forest specialists to escape an open clearcut, but also act as a source of forest specialists to repopulate the area as the forest regenerates (Niemelä et al., 1988; Pohl et al., 2008).

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Appendix A

Checklist of Terrestrial Arthropods, Prince of Wales Island, AK

Arthropods collected on Prince of Wales Island, AK (POW) and surrounding POW islands (Dall Is., Baker Is., Corronation Is., Forrester Is., Heceta Is., Kosciusko Is., Lulu Is., Noyes Is., San Fernando Is., Suemez Is., and Warren Is.) from this project and records from a literature search are included in the checklist below. This list is limited to extant terrestrial or littoral arthropods. The publication and/or museum each taxon is known from, including the determiners who identified the specimens, if known, can be found in the Arctos database at http://arctos.database.museum/saved/POW-Obs for the observation records and http://arctos.database.museum/saved/POW-UAM for the UAM Insect Collection based records. To find all records in Arctos that have been georeferenced to any of these islands, the process for this query is: (1) 'Select on Google Map' in the locality section to set a rectangle on POW for the Arctos search; (2) When results appear, click on 'BerkeleyMapper'; (3) When the results appear, use the draw polygon tool in BerkeleyMapper to isolate the islands around POW; (4) click 'query points inside shape'; (5) click link 'download subset' (This process will eliminate undesired records from the mainland that were in the original Arctos serach); (6) This file can be opened in Microsoft Excel © and saved as .xlsx file; (7) This Excel file can be opened in Filemaker Pro © (FMP) and converted to a FMP database; (8) a script can be made in FMP that will mark duplicate records for deletion (a global field needs to be made, and a 'mark for deletion' field needs to be made; the script starts by sorting all records by their scientific names, goes to the first record, copies the scientific name into the global field, goes to the next record in a loop that exits after the last record, and runs

an ‘if-then’ to compare the scientific name of the current record for deletion by inserting the text ‘delete’ in the ‘mark for deletion’ field, if the names don’t match then it copies that record’s scientific name and pastes it into the global field and moves on to the next record and repeats this process until all duplicate records have been marked for deletion; when the script is done, a search is performed to find those records marked for deletion, and when found, they are deleted. This process reduced over 36,713 records to 1,032 with each record having a unique scientific name not shared by any other; (9) the catalog numbers can then be exported and formatted into a list with all numbers separated by commas with no spaces or returns using MS Word © to query Arctos with the ‘See results as specimen summary’ option to get a list of Class, Order, Family, Genus, and Scientific Name for all records. Two searches were performed, one for the dataset ‘UAM Insects’ which queries all UAM Insect Collection specimen records, and one for the dataset ‘UAM Ento Observations’ which queries all literature and non-UAM Insect Collection records. The above only finds records that have geocoordinates. All records from Southeast Alaska in Arctos that can be georeferenced with any precision have been, so no records should have been missed in the above search. This approach is more reliable than attempting to search using place (island) names because many islands share the same names and different spellings and abbreviations of each island name exist in the data making a name-based search far more error prone.

Prior to the start of this project, from all data sources including published records, we knew of only 100 species of terrestrial arthropods documented from Prince of Wales Island. After the project, we now have 487 species documented from Prince of Wales Island.

Table 13. Prince of Wales Island, Alaska arthropod checklist

CLASS	ORDER	FAMILY (Subfamily)	GENUS / SPECIES	AUTHOR(S)
Arachnida				
	Acarina			
	Araneae			
		Antrodiaetidae		
			Antrodiaetus pacificus	(Simon 1884)
		Amaurobiidae		
			Callobius pictus	(Simon 1884)
			Cybaeopsis wabritaska	(Leech 1972)
			Wadotes sp.	
		Araneidae		
			Araneus nordmanni	(Thorell 1870)
			Araneus saevus	(L. Koch 1872)
			Araneus trifolium	(Hentz 1847)
			Araniella displicata	(Hentz 1847)
			Cyclosa conica	(Pallas 1772)
			Larinioides patagiatus	(Clerck 1757)
			Parazygiella dispar	(Kulczynski 1885)
			Zygiella sp.	
		Clubionidae		
			Clubiona pacifica	Banks 1896
			Clubiona trivialis	C. L. Koch 1843
		Cybaeidae		
			Cybaeota shastae	Chamberlin & Ivie 1937
			Cybaeus morosus	Simon 1886
			Cybaeus reticulatus	Simon 1886
		Dictynidae		
			Cicurina simplex	Simon 1886
			Dictyna brevitarsa	Emerton 1915
			Dicyna major	Menge 1869
		Gnaphosidae		
			Gnaphosa snohomish	Platnick and Shadab 1975
			Micaria pulicaria	(Sundevall 1831)
			Sergiolus montanus	(Emerton 1890)
			Zelotes fratris	Chamberlin 1920

Table 13. Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS / SPECIES	AUTHOR(S)
Arachnida				
	Araneae			
		Hahniidae		
			Antistea brunnea	(Emerton 1909)
			Cryphoeca exlineae	Roth 1988
			Dirksia cinctipes	(Banks 1896)
			Ethobuella tuonops	Chamberlin & Ivie 1937
			Neoantistea magna	(Keyserling 1887)
		Linyphiidae		
			Agnyphantes arboreus	(Emerton 1915)
			Agyneta perspicua	Duperre 2013
			Agyneta protrudens	(Chamberlin & Ivie 1933)
			Aphileta misera	(O. P.-Cambridge 1882)
			Bathyphantes alascensis	(Banks 1900)
			Bathyphantes brevipes	(Emerton 1917)
			Bathyphantes brevis	(Emerton 1911)
			Bathyphantes canadensis	(Emerton 1882)
			Bathyphantes keenii	(Emerton 1917)
			Bathyphantes orica	Ivie 1969
			Bathyphantes pogonias	Kulczynski 1885
			Bathyphantes reprobus	(Kulczynski 1916)
			Centromerus longibulbus	(Emerton 1882)
			Centromerus n.sp.	
			Ceraticelus atriceps	(O. P.-Cambridge 1874)
			Ceraticelus innominabilis	Crosby 1905
			Ceratinella acerea	Chamberlin & Ivie 1933
			Ceratinella alaskae	Chamberlin & Ivie 1947
			Ceratinella ornatula	(Crosby & Bishop 1925)
			Ceratinella tigana	Chamberlin 1948
			Ceratinops inflatus	(Emerton 1923)
			Collinsia ksenia	(Crosby & Bishop 1928)
			Erigone aletris	Crosby & Bishop 1928
			Erigone cristatopalpus	Simon 1884
			Eulaira arctoa	Holm 1960
			Grammonota subarctica	Dondale 1959
			Halorates alascensis	(Banks 1900)
			Islandiana falsifica	(Keyserling 1886)
			Kaestneria rufula	(Hackman 1954)
			Lepthyphantes zibus	Zorsch 1937
			Linyphantes orcinus	(Emerton 1917)
			Linyphantes pualla	Chamberlin & Ivie 1942

Table 13. Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS / SPECIES	AUTHORS(S)
Arachnida				
	Araneae			
		Linyphiidae		
			Meioneta simplex	(Emerton 1926)
			Mermessus trilobatus	(Emerton 1882)
			Metopobactrus pacificus	Emerton 1923
			Micrargus longitarsus	(Emerton 1882)
			Microlinyphia dana	(Chamberlin & Ivie 1943)
			Mythoplastoides erectus	(Emerton 1915)
			Neriene digna	(Keyserling 1886)
			Oedothorax alascensis	(Banks 1900)
			Oreonetides filicatus	(Crosby 1937)
			Oreonetides rotundus	(Emerton 1913)
			Pacifiphantes magnificus	(Chamberlin & Ivie 1943)
			Pelecopsis sculpta	(Emerton 1917)
			Pityohyphantes alticeps	Chamberlin & Ivie 1943
			Pityohyphantes tacoma	Chamberlin & Ivie 1942
			Pocadicnemis pumila	(Blackwall 1841
			Poeciloneta bihamata	(Emerton 1882)
			Poeciloneta canionis	Chamberlin & Ivie 1943
			Poeciloneta fructuosa	(Keyserling 1886)
			Poeciloneta lyrica	(Zorsch 1937)
			Porrhomma convexum	(Westring 1851)
			Saaristoa sammamish	(Levi & Levi 1955)
			Scotinotylus patellatus	(Emerton 1917)
			Sisicottus nesides	(Chamberlin 1921)
			Sisicottus orites	(Chamberlin 1919)
			Sisicottus panopeus	Miller 1999
			Sisis rotundus	(Emerton 1925)
			Symmigma minimum	(Emerton 1923)
			Tachygyna ursine	(Bishop & Crosby 1938)
			Tapinocyba dietrichi	Crosby & Bishop 1933
			Tenuiphantes tenuis	(Blackwall 1852)
			Tenuiphantes zebra	(Emerton 1882)
			Tenuiphantes zelatus	(Zorsch 1937)
			Tenuiphantes zibus	(Zorsch 1937)
			Walckenaeria columbia	Millidge 1983
			Walckenaeria communis	(Emerton 1882)

Table 13. Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS / SPECIES	AUTHORS(S)
Arachnida				
	Araneae			
		Linyphiidae		
			Walckenaeria cornuella	(Chamberlin & Ivie 1939)
			Walckenaeria directa	(O. P.-Cambridge 1874)
			Walckenaeria occidentalis	Millidge 1983
			Walckenaeria spiralis	(Emerton 1882)
			Wubana atypical	Chamberlin & Ivie 1936
			Wubana pacifica	(Banks 1896)
		Lycosidae		
			Arctosa alpigena	(Doleschall 1852)
			Arctosa insignita	(Thorell 1872)
			Arctosa raptor	(Kulczynski 1885)
			Pardosa dorsuncata	Lowrie & Dondale 1981
			Pardosa metlakatla	Emerton 1917
			Pardosa moesta	Banks 1892
			Pirata piraticus	(Clerck 1757)
			Trochosa terricola	Thorell 1856
		Nesticidae		
			Nesticus silvestrii	Fage 1929
		Philodromidae		
			Philodromus rufus	Walckenaer 1826
			Philodromus rufus pacificus	Banks 1898
			Tibellus oblongus	(Walckenaer 1802)
		Pholcidae		
			Pholcus phalangioides	(Fuesslin 1775)
		Pimoidae		
			Pimoa altioculata	(Keyserling 1886)
		Salticidae		
			Evarcha proszynskii	Marusik Logunov 1997 [1998]
			Neon reticulatus	(Blackwall 1853)
			Pelegrina aeneola	(Curtis 1892)
		Telemidae		
			Usofila pacifica	(Banks 1894)
			Metellina curtisi	(McCook 1894)
			Tetragnatha extensa	(Linneaus 1758)

Table 13. Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS / SPECIES	AUTHORS(S)
Arachnida				
	Araneae			
		Tetragnathidae		
			Tetragnatha laboriosa	Hentz 1850
			Tetragnatha versicolor	Walckenaer 1842
		Theridiidae		
			Robertus vigerens	(Chamberlin & Ivie 1933)
			Rugathodes sexpunctatus	(Emerton 1882)
			Theonoe stridula	Crosby 1906
			Theridion saanichum	Chamberlin & Ivie 1947
		Thomisidae		
			Misumena vatia	(Clerck 1757)
			Xysticus pretiosus	Gertsch 1934
		Uloboridae		
			Hyptiotes gertschi	Chamberlin & Ivie 1935
	Ixodida			
		Ixodidae		
			Ixodes uriae	White 1852
	Opiliones			
		Ceratolasmatidae		
			Hesperonemastoma modestum	(Banks 1894)
		Nemastomatidae		
			Dendrolasma mirabile	Banks 1894
		Phalangiidae		
			Phalangium opilio	Linnaeus 1758
		Sabaconidae		
			Sabacon occidentalis	(Banks 1894)
		Sclerosomatidae		
			Nelima paessleri	(Roewer 1910)
		Triaenonychidae		
			Paranonychus brunneus	(Banks 1893)
	Prostigmata			
		Rhagidiidae		

Table 13. Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS / SPECIES	AUTHORS(S)
Arachnida				
	Pseudoscorpiones			
		Neobisiida		
			Halobisium occidentale	Beier 1931
	Sarcoptiformes			
		Cepheidae		
			Eupterotegaeus sp.	
		Liacaridae		
			Liacarus sp.	
Chilopoda				
	Geophilomorpha			
	Lithobiomorpha			
		Lithobiidae		
			Oabius uleorus	Chamberlin 1916
			Paobius boreus	Chamberlin 1916
			Zygethopolys nothus	Chamberlin 1925
Diplopoda				
	Polydesmida			
		Xystodesmidae		
			Harpaphe haydeniana	(Wood 1864)
	Polyxenida			
		Polyxenidae		
			Polyxenus lagurus	(Linnaeus 1758)
	Julida			
Pauropoda				
Insecta				
	Collembola			
		Hypogastruridae		
			Brachystomella sp.	
			Hypogastrura glancei	(Hammer 1953)
			Paranura colorata	Mills 1934
		Onychiuridae		
			Onychiurus millsi	Chamberlain 1943
			Onychiurus pseudarmatus	Folsom 1917
			Onychiurus ramosus	Folsom 1917

Table 13. Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS / SPECIES	AUTHORS(S)
Insecta				
	Collembola			
		Onychiuridae		
			Onychiurus sibiricus	(Tulberg 1876)
		Isotomidae		
			Folsomia candida	Willem 1902
		Entomobryidae		
			Tomocerus flavescens	(Tullberg 1871)
		Sminthuridae		
			Arrhopalites diversus	Mills 1934
			Arrhopalites hirtus	Christiansen 1966
			Dicyrtoma palmate	Folsom 1902)
			Ptenothrix atra	(Linnaeus 1758)
	Archaeognatha			
		Machilidae		
			Pedetontus sp. prob. *submutans*	(Silvestri 1911)
			Petridiobius arcticus	(Folsom 1902)
	Ephemeroptera			
		Ameletidae		
			Ameletus sp.	
		Baetidae		
			Baetis sp.	
		Ephemerellidae		
			Drunella doddsi	(Needham 1927)
			Drunella grandis	(Eaton 1884)
		Heptageniidae		
			Cinygma sp.	
			Cinygmula sp.	
			Epeorus longimanus	(Eaton 1885)
			Rhithrogena sp.	
		Leptophlebiidae		
			Paraleptophlebia sp.	
	Odonata			
		Aeshnidae		
			Aeshna subarctica	Walker 1908
		Coenagrionidae		
			Zoniagrion sp.	
	Orthoptera			
		Rhaphidophoridae		
			Pristoceuthophilus cercalis	Caudell 1916

Table 13. Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS / SPECIES	AUTHORS(S)
Insecta				
	Plecoptera			
		Nemouridae		
			Visoka cataractae	(Neave 1933)
			Podmosta weberi	(Ricker 1952)
			Zapada cinctipes	(Banks 1897)
			Zapada columbiana	(Claassen 1923)
		Leuctridae		
			Despaxia augusta	(Banks 1907)
		Capniidae		
			Capnia melia	Frison 1942
		Perlidae		
			Hesperoperla pacifica	(Banks 1900)
		Chloroperlidae		
			Suwallia starki	Alexander & Stewart 1999
			Sweltsa revelstoka	(Jewett 1955)
	Hemiptera			
		Ceratocombidae		
			Ceratocombus vagans	(McAtee & Malloch 1925)
		Gerridae		
			Gerris incognitus	(Drake & Hottes 1925)
		Belostomatidae		
			Lethocerus americanus	(Leidy 1847)
		Corixidae		
			Callicorixa alaskensis	Hungerford 1926
		Saldidae		
			Saldula laticollis	(Reuter 1875)
		Miridae		
			Orthops scutellatus	Uhler 1877
		Cicadellidae		
		Delphacidae		
			Javesella pellucida	(Fabricius 1794)
		Cixiidae		
			Cixius sp.	
		Psyllidae		
		Aphididae		
			Macrosiphum sp.	
			Cinara sp.	

Table 13. Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS / SPECIES	AUTHORS(S)
Insecta				
	Hemiptera			
		Ortheziidae		
			Arctorthezia cataphracta	(Olafsen 1772)
		Coccidae		
	Thysanoptera			
	Psocoptera			
	Coleoptera			
		Carabidae		
		(Nebriinae)	*Leistus ferruginosus*	Mannerheim 1843
			Nebria sp.	
			Notiophilus sylvaticus	Eschscholtz 1833
		(Carabinae)	*Carabus taedatus*	Fabricius 1787
			Cychrus tuberculatus	Harris 1839
			Scaphinotus angusticollis	(Fischer von Waldheim 1823)
			Scaphinotus marginatus	(Fischer von Waldheim 1820)
		(Loricerinae)	*Loricera decempunctata*	Eschscholtz 1833
		(Trechinae)	*Amerizus oblongulus*	(Mannerheim 1852)
			Amerizus spectabilis	(Mannerheim 1852)
			Bembidion dyschirinum	(LeConte 1861)
			Trechus chalybeus	Dejean 1831
		(Harpalinae)	*Amara littoralis*	Mannerheim 1843
			Bradycellus nigrinus	(Dejean 1829)
			Pterostichus adstrictus	Eschscholtz 1823
			Pterostichus algidus	LeConte 1852
			Pterostichus amethystinus	Mannerheim 1843
			Pterostichus castaneus	(Dejean 1828)
			Pterostichus crenicollis	LeConte 1873
			Pterostichus riparius	Dejean 1828)
		Gyrinidae		
			Gyrinus sp.	
		Dytiscidae		
			Agabus tristis	Aube 1838
			Hydaticus sp.	
			Sanfilippodytes sp.	
		Hydrophilidae		
			Ametor latus	(Horn 1873)
			Cercyon sp.	
			Helophorus auricollis	(Eschscholtz 1822)

Table 13. Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS / SPECIES	AUTHORS(S)
Insecta				
	Coleoptera			
		Sphaeritidae		
			Sphaerites politus	Mannerheim 1846
		Histeridae		
			Paromalus mancus	Casey 1893
		Hydraenidae		
			Neochthebius vandykei	(Knisch 1924)
		Ptiliidae		
			Actidium crotchianum	Matthews 1877
		Agyrtidae		
			Necrophilus hydrophiloides	Guerin-Meneville 1835
		Leiodidae		
			Agathidium sp.	
			Anogdus sp.	
			Catops sp.	
			Colon magnicolle	Mannerheim 1853
			Leiodes sp.	
			Leptinus occidentamericanus	Peck 1982
			Pinodytes cryptophagoides	(Mannerheim 1852)
			Ptomaphagus sp.	
			Triarthron lecontei	Horn 1868
		Scydmaenidae		
			Lophioderus sp.	
		Silphidae		
			Nicrophorus defodiens	Mannerheim 1846
			Nicrophorus investigator	Zetterstedt 1824
		Staphylinidae (Omaliinae)	*Acidota crenata*	(Fabricius)
			Acruliopsis n.sp. II	
			Amphichroum c.f. *maculatum*	(Horn 1882)
			Anthobium sp.	
			Carcinocephalus exsculpta	(Mäklin 1852)
			Deinopteroloma subcostatum	(Mäklin 1852)
			Dropephylla longula	(Mäklin 1852)
			Eusphalerum sp.	
			Hapalaraea sp.	
			Omalium sp.	

Table 13. Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS / SPECIES	AUTHORS(S)
Insecta				
	Coleoptera			
		Staphylinidae		
		(Omaliinae)	*Orobanus falli*?	Mank 1934
			Pelecomalium testaceum	(Mannerheim 1843)
			Phlaeopterus fusconiger	Motschulsky 1853
			Phlaeopterus houkae	Hatch 1957
			Phlaeopterus lagrandeuri	Hatch 1957
			Phloeonomus laesicollis	(Mäklin 1852)
			Phloeonomus suffuses	(Casey)
			Phyllodrepa strigipennis	(Mäklin 1852)
			Pseudohaida sp.	
			Tanyrhinus singularis	Mannerheim 1852
			Unamis fulvipes	(Fall 1922)
		(Proteininae)	*Megarthrus pictus*	Motschulsky 1845
			Proteinus basalis	Mäklin 1852
			Proteinus collaris	Hatch 1957
		(Micropeplinae)	*Arrhenopeplus tesserula*	(Curtis 1828)
			Micropeplus brunneus	Mäklin 1852
			Micropeplus punctatus	LeConte 1863
		(Pselaphinae)	*Actium* sp.	
			Batrisodes albionicus	(Aube 1833)
			Cupila clavicornis	(Mäklin 1852)
			Foveoscapha terracola	Park & Wagner 1961
			Lucifotychus cognatus	(LeConte 1874)
			Pselaphinae sp.	
			Reichenbachia binodifer	Casey 1897
			Sonoma Cascadia	Chandler 1986
			Sonoma margemina	Park & Wagner 1962
			Sonoma parviceps	(Mäklin 1852)
			Trimioplectus sp.	
		(Tachyporinae)	*Bolitobius cingulatus*	Mannerheim 1831
			Bryophacis biseriatus	(Mannerheim 1846)
			Bryophacis punctatissimus ?	(Hatch 1957)

Table 13. Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS / SPECIES	AUTHORS(S)
Insecta				
	Coleoptera			
		Staphylinidae		
		(Tachyporinae)	*Bryophacis smetanai*?	Campbell 1993
			Carphacis sp.	
			Lordithon thoracicus	(Fabricius 1777)
			Mycetoporus rufohumeralis?	Campbell 1991
			Mycetoporus rugosus	Hatch 1957
			Tachinus basalis	Erichson 1839
			Tachinus maculicollis	Mäklin 1852
			Tachinus semirufus	Horn 1877
		(Trichophyinae)	*Trichophya pilicornis*	(Gyllenhal 1810)
		(Harbrocerinae)	*Oxypoda frigida*	Bernhauer 1907
			Oxypoda grandipennis	(Casey 1911)
			Oxypoda longicarinata	Klimaszewski 2006
		(Aleocharinae)	*Aleochara sulcicollis*	Mannerheim 1843
			Aloconota cambric	(Wollaston 1855)
			Atheta brumalis	Casey 1910
			Atheta circulicollis	Lohse 1990
			Atheta hampshirensis	Bernhauer 1909
			Atheta irrupta	(Casey 1910)
			Atheta keeni	Casey 1910
			Atheta metlakatlana	Bernhauer 1909
			Atheta nescia	(Casey 1910)
			Atheta picipennis	(Mannerheim 1843)
			Atheta pseudosubtilis	Klimaszewski & Langor 2011
			Atheta riparia	Klimaszewski 2012
			Atheta stercoris	Fenyes 1920
			Atheta strigosula	Casey 1910
			Atheta ventricosa	Bernhauer 1907
			Autalia truncatula	Casey 1911
			Boreostiba sp.	
			Clusiota antennalis	Klimaszewski & Godin 2008
			Gnathusa tenuicornis	Fenyes 1921
			Gyrophaena keeni	Casey 1911
			Liogluta n.sp.	

Table 13. Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS / SPECIES	AUTHORS(S)
Insecta				
	Coleoptera			
		Staphylinidae		
		(Aleocharinae)	*Liogluta nitens*	(Mäklin and Mannerheim 1852)
			Lypoglossa angularis angularis	(Mäklin and Mannerheim 1853)
			Mniusa yukonensis	(Klimaszewski & Godin 2012)
			Mocyta fungi	(Gravenhorst 1806)
			Neothetalia columbiana	(Klimaszewski 2002)
			Neothetalia nimia	(Casey 1910)
			Philhygra angusticauda	(Bernhauer 1909)
			Philhygra laevicollis	(Mäklin in Mannerheim 1852)
			Placusa tacomae	Casey 1893
			Schistoglossa campbelli	Klimaszewski 2009
			Silusa californica	(Bernhauer 1905)
			Silusa vesperis	Casey 1893
			Stictalia californica	(Casey 1885)
		(Oxytelinae)	*Ochthephilus biimpressus*	(Mäklin 1852)
			Oxytelus fuscipennis	Mannerheim 1843
			Oxytelus laqueatus	(Marsham 1802)
			Syntomium sp.	
			Thinobius sp.	
		(Steininae)	*Stenus pterobrachys*	Gemminger & Harold 1868
		(Staphylininae)	*Atrecus macrocephalus*	(Nordmann 1837)
			Atrecus quadripennis	(Casey 1906)
			Beeria nematocera	(Casey 1915)
			Bisnius sp.	
			Parothius californicus	(Mannerheim 1843)
			Parothius punctatus	Smetana 1982
			Quedius plagiatus	Mannerheim1846
			Quedius pullmani	Hatch 1957
			Quedius transparens	Motschulsky 1845
		Lucanidae		
			Ceruchus striatus	LeConte 1859
		Scarabaeidae		
			Aegialia cylindrical	(Eschscholtz 1822)
			Agoliinus leopardus	(Horn 1870)
			Agoliinus piceatus	(Robinson 1946)
			Caelius browni	(Saylor 1934)

Table 13. Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS / SPECIES	AUTHORS(S)
Insecta				
	Coleoptera			
		Scarabaeidae		
			Planolinoides borealis	(Gyllenhal 1827)
			Planolinoides duplex	(LeConte 1878)
		Byrrhidae		
			Cytilus sp.	
			Exomella pleuralis	(Casey 1908)
			Lioligus nitidus	(Motschulsky 1845)
			Lioon simplicipes	(Mannerheim 1852)
			Listemus acuminatus	(Mannerheim 1852)
		Elmidae		
			Narpus sp.	
		Ptilodactylidae		
			Araeopidius monachus	(LeConte 1874)
		Eucnemidae		
			Epiphanis cornutus	Eschscholtz 1829
		Elateridae		
			Ampedus apicatus	(Say 1839)
			Ampedus carbonicolor	(Eschscholtz 1829)
			Athous rufiventris	(Eschscholtz 1822)
			Ctenicera angusticollis	(Mannerheim 1843)
			Ctenicera sp.	
			Idolus debilis	(LeConte 1884)
			Liotrichus sagitticollis	(Eschscholtz 1829)
			Liotrichus umbricolus	(Eschscholtz 1829)
			Liotrichus volitans	(Eschscholtz 1829)
			Nitidolimonius resplendens	(Eschscholtz 1829)
		Lycidae		
			Dictyoptera aurora	(Herbst 1784)
			Dictyoptera simplicipes	Mannerheim 1843
			Punicealis hamate	(Mannerheim 1843)
		Cantharidae		
			Dichelotarsus piniphilus or *Dichelotarsus flavimanus*	(Eschscholtz 1830)
			Silis sp.	
		Derodontidae		
			Derodontus trisignatus	(Mannerheim 1852)
			Peltastica tuberculate	Mannerheim 1852
		Anobiidae		

Table 13. Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS / SPECIES	AUTHORS(S)
Insecta				
	Coleoptera			
		Trogossitidae		
			Calitys scabra	(Thunberg 1784)
			Peltis pippingskoeldi	(Mannerheim 1852)
		Cleridae		
			Thanasimus sp.	
		Nitidulidae		
			Epuraea aestiva	(Linnaeus 1758)
			Epuraea pallescens	Erichson 1843
			Epuraea planulata	Erichson 1843
		Monotomidae		
			Rhizophagus dimidiatus	(Mannerheim 1843)
			Rhizophagus grouvellei	Mequignon 1913
			Rhizophagus sculpturatus	Mannerheim 1842
		Silvanidae		
			Dendrophagus cygnaei	Mannerheim 1846
		Cucujidae		
			Cucujus clavipes	Fabricius 1777
		Cryptophagidae		
			Atomaria nr. *affinis*	Sahlberg 1834
			Atomaria nr. *ornata*	Heer 1841
			Cryptophagus sp.	
			Henotiderus lorna	(Hatch 1962)
			Henotiderus n.sp	
			Pteryngium crenatum	(Gyllenhal 1827)
			Salebius sp.	
		Latridiidae		
			Aridius sp.	
			Cartodere nodifer	(Westwood 1839)
			Corticaria sp.	
			Enicmus cordatus	Belon 1895
		Ciidae		
			Cis fuscipes	Mellié 1848
			Orthocis sp.	
		Melandryidae		
			Lederia arctica	(Horn 1893)
			Orchesia sp.	
			Prothalpia holmbergi	(Mannerheim 1852)
			Serropalpus substriatus	Haldeman 1848
		Colydiidae		

Table 13. Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS / SPECIES	AUTHORS(S)
Insecta				
	Coleoptera			
		Zopheridae		
			Phellopsis porcata	LeConte 1853
		Tenebrionidae		
		Oedemeridae		
			Ditylus gracilis	LeConte 1854
			Ditylus quadricollis	LeConte 1851
		Stenotrachelidae		
			Cephaloon bicolor	Horn 1896
		Pythidae		
			Priognathus monilicornis	(Randall 1838)
			Pytho niger	Kirby 1837
		Salpingidae		
			Aegialites sp.	
			Rhinosimus viridiaeneus	(Randall 1838)
		Scraptiidae		
			Anaspis rufa	Say 1826
			Anaspis sericea	Mannerheim 1843
		Cerambycidae		
			Evodinus monticola	(Randall 1838)
			Opsimus quadrilineatus	Mannerheim 1843
			Plectrura spinicauda	Mannerheim 1852
			Rhagium inquisitor	(Linnaeus 1758)
			Tetropium sp.	
			Ulochaetes leoninus	LeConte 1854
			Xestoleptura crassipes	(LeConte 1857)
		Chrysomelidae		
			Syneta carinata	Mannerheim 1843
		Curculionidae		
			Alniphagus aspericollis	(LeConte 1876)
			Cossonus sp.	
			Dendroctonus rufipennis	(Kirby 1837)
			Dolurgus pumilus	(Mannerheim 1843)
			Dryocoetes affaber	(Mannerheim 1852)
			Dryocoetes autographus	(Ratzeburg 1837)
			Gnathotrichus retusus	(LeConte 1868)
			Hylobius warren	Wood 1957
			Hylurgops rugipennis	(Mannerheim 1843)
			Ips tridens	(Mannerheim 1852)
			Lepidophorus sp.	

Table 13. Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS / SPECIES	AUTHOR(S)
Insecta				
	Coleoptera			
		Curculionidae		
			Nemocestes horni	Van Dyke E.C. 1936
			Phloeosinus punctatus	LeConte 1876
			Phloeosinus sequoia	Hopkins 1903
			Pissodes costatus	Mannerheim 1852
			Pityophthorus nitidulus	(Mannerheim 1843)
			Pseudips concinnus	Cognato 2000
			Pseudohylesinus sericeus	(Mannerheim 1843)
			Pseudohylesinus tsugae	Swaine 1917
			Rhyncolus brunneus	Mannerheim 1843
			Steremnius carinatus	(Boheman 1842)
			Steremnius tuberosus	Gyllenhal 1836
			Sthereus horridus	(Mannerheim 1852)
			Sthereus multituberculatus	Buchanan 1936
			Sthereus quadrituberculatus	Motschulsky 1845
			Trichalophus didymus	(LeConte 1856)
			Trypodendron lineatum	Wood & Bright 1992
	Neuroptera			
		Hemerobiidae		
	Hymenoptera			
		Argidae		
			Arge clavicornis	(Fabricius 1781)
		Diprionidae		
			Neodiprion abietis complex	
			Neodiprion tsugae	Middleton 1933
		Tenthredinidae		
			Amauronematus sp.	
			Melastola ferruginosa	Wong 1968
			Pachynematus vagus	(Fabricius 1781)
			Pikonema dimmockii?	(Cresson 1880)
			Pikonema ruralis	(Cresson 1880)
			Pristiphora mollis	(Hartig 1837)
			Tenthredo varipicta	Norton 1868

Table 13. Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS / SPECIES	AUTHOR(S)
Insecta				
	Hymenoptera			
		Siricidae		
			Sirex cyaneus	Fabricius 1781
			Xeris caudatus	(Cresson 1865)
		Braconidae		
			Aphidius sp.	
			Meteorus argyrotaeniae	Johansen 1949
		Ichneumonidae		
			Agrypon sp.	
			Aphanistes sp.	
			Aptesini sp.	
			Bathythrix latifrons	(Cushman 1939)
			Cratichneumon pteridis	Townes 1944
			Delomerista diprionis	Cushman 1939
			Exochus decorates	Holmgren 1873
			Gelis tenellus	(Say 1835)
			Hercus fontinalis?	(Holmgren 1857)
			Itoplectis quadricingulatus	(Provancher 1880)
			Lamachus sp.	
			Lissonota sp.	
			Mastrus aciculatus	(Provancher 1886)
			Mastrus hydrophilus	(Ashmead 1890)
			Mesochorus sp.	
			Netelia sp.	
			Oresbius tsugae	(Cushman 1939)
			Orthocentrus sp.	
			Phaeogenes arcticus	Cushman 1920
			Pimpla Hesperus	(Townes 1960)
			Stenomacrus sp.	
			Theroscopus sp.	

Table 13. Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS / SPECIES	AUTHOR(S)
Insecta				
	Hymenoptera			
		Eulophidae		
			Elachertus cacoeciae	Howard 1885
			Ichneumon sp.	
		Torymidae		
			Megastigmus atedius	Walker 1851
			Megastigmus tsugae	Crosby 1913
		Pteromalidae		
			Mesopolobus verditer	(Norton 1869)
		Proctotrupidae		
		Apidae		
			Bombus insularis	(Smith 1861)
			Bombus melanopygus	Nylander 1848
			Bombus sitkensis	Nylander 1848
			Bombus sylvicola	Kirby 1837
		Vespidae		
			Dolichovespula arenaria	(Fabricius 1775)
			Dolichovespula norvegicoides	(Sladen 1918)
			Vespula sp.	
		Formicidae		
	Trichoptera			
		Philopotamidae		
			Wormaldia sp.	
		Glossosomatidae		
		Rhyacophilidae		
			Rhyacophila sp.	
		Limnephilidae		
			Dicosmoecus atripes	(Hagen 1875)
			Onocosmoecus unicolor	(Banks 1897)
			Psychoglypha sp.	
	Lepidoptera			
		Argyresthiidae		
			Argyresthia tsuga	Freeman 1972
		Tortricidae		
			Choristoneura fumiferana	(Clemens 1865)
			Clepsis porsicana	(Fitch 1856)
			Acleris gloveranus	Walsingham 1879

Table 13. Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS / SPECIES	AUTHOR(S)
Insecta				
	Lepidoptera			
		Pieridae		
			Pieris oleracea?	(Harris 1829)
			Pieris marginalis	Scudder 1861
		Nymphalidae		
			Boleria epithore	(W.H. Edwards 1864)
		Drepanidae		
			Habrosyne scripta	Gosse 1840
		Geometridae		
			Enypia venata	Grote 1883
			Mesoleuca sp.	
		Sphingidae		
			Hyles galli	(Rottemburg 1775)
		Noctuidae		
			Anaplectoides prasina	(Denis & Schiffermüller 1775)
			Noctua pronuba	Linnaeus 1758
	Mecoptera			
		Boreidae		
			Caurinus tlagu	Sikes & Stockbridge 2013
	Diptera			
		Tipulidae		
			Austrolimnophila badia	(Doane 1900)
			Dicranota maculate	(Doane 1900)
			Limnophila indistincta	Doane 1900
		Tipulidae		
			Limnophila vancouverensis	Alexander 1943
			Limonia nubeculosa	Meigen 1804
			Molophilus falcatus	Bergroth 1888
			Ormosia sp.	
			Pedicia sp.	
			Tipula subtenuicornis	Doane 1901
		Pediciidae		
			Tricyphona protea	Alexander 1918
		Psychodidae		
			Pericoma sp.	
		Ceratopogonidae		

Table 13. Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS / SPECIES	AUTHOR(S)
Insecta				
	Diptera			
		Chironomidae		
			Boreochlus sp.	
			Eukiefferiella sp.	
			Forcipomyia sp.	
			Krenopelopia sp.	
			Metriocnemus sp.	
			Micropsectra sp.	
			Orthocladius sp.	
			Parametriocnemus sp.	
			Paraphaenocladius sp.	
			Probezzia sp.	
			Rheotanytarsus sp.	
			Tanytarsus sp.	
			Thalassosmittia sp.	
			Thienemanniella sp.	
			Trissopelopia sp.	
		Culicidae		
		Dixidae		
			Dixella sp.	
		Simuliidae		
			Parasimulium sp.	
			Simulium sp.	
		Anisopodidae		
			Sylvicola fuscatus	(Fabricius 1775)
		Bibionidae		
			Bibio rufipes?	Zetterstedt 1838
			Dilophus femoratus?	Meigen 1804
		Cecidomyiidae		
			Contarinia sp.	
			Corinthomyia sp.	
			Janetiella sp.	
			Thecodiplosis sp.	
		Mycetophilidae		
			Acnemia similis	Zaitzev 1982
			Boletina imitator	Johannsen 1912
			Bolitophila sp.	
			Brevicornu sp.	
			Coelophthinia sp. nov?	
			Diadocidia sp. nov. cf. *borealis*	
			Dziedzickia sp. nov.	

Table 13. Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS / SPECIES	AUTHOR(S)
Insecta				
	Diptera			
		Mycetophilidae		
			Exechia sp.	
			Exechiopsis sp.	
			Macrocera sp.	
			Macrocera sp. nov.	
			Mycetophila paula	(Loew 1869)
			Mycetophila ruficollis	Meigen 1818
			Mycomya pura	Vaisanen 1984
			Mycomya terminate	Garrett 1924
			Neuratelia sp. nov. cf. *silvatica*	
			Orfelia mendosa	(Loew 1869)
			Phronia flavipes	Winnertz 1863
			Phronia sp. nov. gr. *tarsata*	(Staeger 1840)
			Phthinia sp. nov.	
			Rymosia sp.	
			Symmerus sp.	
			Synapha astacus	Garrett 1924
			Synapha disjuncta	(Garrett 1925)
			Synapha sp.	
		Ditomyiidae		
			Symmerus coqulus	Garrett 1925
		Diadocidiidae		
			Diadocidia trispinosa	Polevoi 1996
		Pachyneuridae		
			Cramptonomyia spenceri	Alexander 1931
		Scatopsidae		
		Sciaridae		
			Bradysia sp.	
			Pnyxia sp.	
		Empididae		
			Anthalia sp.	
			Clinocera sp.	
			Oreothalia sp.	
		Dolichopodidae		
			Dolichopus groenlandicus	Zetterstedt 1843
			Gymnopternus sp.	
		Lonchopteridae		
		Phoridae		
			Lecanocerus sp.	

Table 13. Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS / SPECIES	AUTHOR(S)
Insecta				
	Diptera			
		Phoridae		
			Pericyclocera sp.	
		Platypezidae		
		Syrphidae		
			Blera flukei	(Curran 1953)
			Blera scitula	(Williston 1882)
			Cheilosia lasiophthalmus	Williston 1882
			Hiatomyia sp.	
			Melangyna lasiophthalma	(Zetterstedt 1843)
			Melanostoma mellinum?	(Linnaeus 1758)
			Parasyrphus tarsatus	Macquart 1842
			Platycheirus flabella	Hull 1944
			Platycheirus holarcticus?	Vockeroth 1990
			Platycheirus hyperboreus?	(Staeger 1845)
			Platycheirus peltatoides?	Curran 1923
			Platycheirus sp.	
			Sericomyia chalcopyga	Loew 1863
			Xylota barbata	Loew 1864
		Anthomyiidae		
			Acridomyia sp.	
		Calliphoridae		
			Calliphora sp.	
			Cynomya cadaverina	Robineau-Desvoidy 1830
			Tricampa rileyi	Silvestri 1933
		Fanniidae		
		Muscidae		
			Mesembrina latreillii	Robineau-Desvoidy 1830
		Sarcophagidae		
		Scathophagidae		
			Allomyella borealis	Curran 1927
			Scathophaga furcate	(Say 1823)
		Tachinidae		
		Lonchaeidae		
			Lonchaea zetterstedti	Becker 1902
		Lauxaniidae		
		Dryomyzidae		
			Dryomyza sp.	
			Oedoparena sp.	

Table 13. Continued.

CLASS	ORDER	FAMILY (Subfamily)	GENUS / SPECIES	AUTHOR(S)
Insecta				
	Diptera			
		Sciomyzidae		
		Heleomyzidae		
		Sphaeroceridae		
			Aptilotus sp.	
			Crumomyia sp.	
Malacostraca				
	Decapoda			
		Paguridae		
			Pagurus ochotensis	Brandt 1851
	Isopoda			
		Aegidae		
			Rocinela belliceps	(Stimpson 1864)
	Amphipoda			
		Ampithoidae		
			Peramphithoe humeralis	(Stimpson 1864)
		Crangonyctidae		
			Crangonyx richmondensis	Ellis 1940
			Stygobromus sp.	
		Gammaridae		
			Gammarus lacustris	G. O. Sars 1863
		Hyalellidae		
			Hyalella Azteca	Saussure 1858
Maxillopoda				
	Cyclopoida			
		Cyclopidae		
			Acanthocyclops capillatus	(G. O. Sars 1863)
			Diacyclops sp.	
		Copepoda		
Ostracoda				
	Podocopida			
		Candonidae		
			Candona sp.	

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Appendix B

Description of *Caurinus tlagu*, new species, from Prince of Wales Island, Alaska (Mecoptera, Boreidae, Caurininae)

Derek S. Sikes and Jill Stockbridge

Abstract

A new species of the cryptic, minute, wingless, and enigmatic taxon *Caurinus*, and the second for the subfamily Caurininae, is described from Prince of Wales Island in the Alexander Archipelago, Alaska. It is distinguished from its only congener, *Caurinus dectes* Russell, 1979b, which occurs 1, 059 km southeast in Oregon and Washington, based on external morphology and sequences of the mitochondrial gene cytochrome oxidase II. These two species are probably evolutionary relicts – the only known members of a clade dating to the Late Jurassic or older.

Introduction

Russell (1979a, b, 1982) described the monotypic subfamily Caurininae, genus and species *Caurinus dectes*, known only from Oregon and Washington, and later described by Beutel, Friedrich, and Whiting (2008) as “arguably one of the most bizarre and cryptic species of Mecoptera and endopterygote insects.” Indeed, members of the genus do not key to any order in most keys to insect orders because they lack a produced rostrum, typical of the order Mecoptera, and lack the diagnostic traits that would place them within *any* insect order containing flightless adults with rudimentary or vestigial wings. However, they do share with members of the family Boreidae a very

distinctive wing morphology and sexual dimorphism in which the adult females are nearly wingless while the males bear shortened scissor-like wings, useless for flight, that bear spines for grasping females during mating. The placement of *Caurinus* within the Mecopteran family Boreidae as the sister taxon to the Boreinae (*Boreus* 26 spp., *Hesperoboreus* 2 spp. [Penny, 2013]), is apparently well established based on morphological study (Russell, 1979a, b; Beutel et al., 2008, Friedrich, Pohl, Beckmann, & Beutel, 2013) and molecular phylogenetics (Whiting, 2002). However, despite recent efforts, the genus remains enigmatic due to its preponderance of plesiomorphic and autapomorphic traits (Beutel et al., 2008). The close relationship of the Mecoptera with the fleas, order Siphonaptera, is of particular evolutionary interest (Grimaldi & Engel, 2005; Whiting, 2002; Trautwein, Wiegmann, Beutel, Kjer, Yeates, 2012).

It was therefore with some excitement that we began accumulating *Caurinus* specimens from a large sampling project on the northern end of Prince of Wales Island, Alaska, some 1, 059 km from the known range of *Caurinus dectes* Russell. Herein we describe this new species.

Materials and methods

Collections. Specimens will be deposited in the following collections:

CAS California Academy of Sciences, San Francisco, California, USA. (Norm Penny)

MTEC Montana Entomology Collection, Bozeman, Montana, USA. (Michael Ivie)

OSAC Oregon State Arthropod Collection, Oregon State University, Corvallis, Oregon, USA. (David R. Maddison)

PMJ Phyletisches Museum, Jena, Germany (Rolf G. Beutel)

SEMC Snow Entomological Museum, University of Kansas, Lawrence, Kansas, USA. (George Byers)

UAM University of Alaska Museum Insect Collection, University of Alaska, Fairbanks, Alaska, USA. (Derek S. Sikes)

USNM National Museum of Natural History, Washington D.C., USA. (Ollie Flint)

Morphological methods. Images of *Caurinus tlagu* were captured using a Leica DFC425 camera mounted on a Leica MZ16 stereomicroscope in combination with Leica Application Suite © software v.3.8.0. Images were edited using Adobe Photoshop v.7 to remove the background and lighten the images. Observations were made with a Leica MZ16 stereomicroscope (7.1×–115× magnification, 1x planapochromatic objective/10× eyepieces, max resolution 420 Lp/mm, Leica Microsystems (Switzerland) Ltd.). Measurements were made using an ocular micrometer in the MZ16 scope at 50×. Five *Caurinus tlagu* specimens were prepared for scanning electron microscopy (SEM) using a Tousimis Samdri-790 Critical Point Dryer and sputter (gold) coating with a Ladd coating unit. The scanning electron micrographs were taken with a ISI-SR-50 SEM and the digital imaging program Iridium Digital Imaging System. In addition to the images included herein, many more SEMs and habitat photos are associated with their specimen records via our online database Arctos (http://arctos.database.museum/saved/Caurinus-spp).

Taxon sampling. Two Mecoptera COII sequences from GenBank were used as outgroups: *Boreus westwoodi* Hagen (EU335963.1) and *Boreus hyemalis* (L.) (AF423998.1). *Boreus* species were chosen because they share the family assignment

of Boreidae with *Caurinus* and therefore should be more closely related to *Caurinus* than any other genus in GenBank. The single *Caurinus dectes* COII sequence on GenBank (AF424001.1) was initially included (and its existence drove our desire to sequence COII rather than the more common gene COI), but later excluded due to it being suspected of errors (see below). One of the five Alaskan *Caurinus* specimens had ambiguous reads in both directions for its COII sequence, possibly due to co-amplification of a nuclear copy. We excluded this sequence from analysis.

Caurinus dectes specimens were provided by L. Russell. Seven specimens from Lewis County, Washington, collected in 1978 were provided for morphological study and 12 larval and 11 adult specimens from 2012 collections made in Benton and Tillamook Counties, Oregon, for DNA analysis (Table 14). Our collecting efforts on Prince of Wales Island have yielded 37 specimens (18 males, 19 females) of *Caurinus tlagu* (see Collecting methods below, Table 1). Additional, non-type specimens are likely to be found as sampling progresses. These specimens will be archived in UAM and recorded in our online database, Arctos.

Table 14. Specimen data (n=50 lots). Also available online at http://arctos.database.museum/saved/Caurinus-spp via Arctos. Geocoordinates are in WGS84 datum. PoW = Prince of Wales Island. * = holotype male *Caurinus tlagu*, with genitalia everted and COII gene sequenced. All other *Caurinus tlagu* specimens are paratypes. W-screen = wet screen, Hab. = habitat. Habitat type codes: T2 = thinned secondary growth, 2= young secondary growth (unthinned), 2o = old (80yr) secondary growth, CC = clearcut, CCe = clearcut / forest ecotone, OG = old growth, AH = alpine heath. Date1 and Date2 = start and stop dates for trap samples.

Catalog Number	Species	State	Locality	Hab.	Method	Date1	Date2	Latitude	Longitude	+/- (m)	sex / stage
UAM:Ento:121022	*C. tlagu*	Alaska	PoW Is. Coffman Cv	T2	pitfall	4/27/10	5/15/10	55.9795	-132.86256	101	male
UAM:Ento:121023	*C. tlagu*	Alaska	PoW Is. Coffman Cv	T2	Berlese	5/13/10		55.9795	-132.86256	101	female
UAM:Ento:135813	*C. tlagu*	Alaska	PoW Is. Coffman Cv	T2	pitfall 4	5/14/10	5/28/10	55.9795	-132.86256	101	male
UAM:Ento:159146	*C. tlagu*	Alaska	PoW Is. Coffman Cv	T2	pitfall 2	7/14/10	7/26/10	55.9795	-132.86256	101	male
UAM:Ento:202339	*C. tlagu*	Alaska	PoW Is. Coffman Cv	T2	pitfall 4	5/18/11	5/31/11	55.9795	-132.86256	101	female , male
UAM:Ento:204005	*C. tlagu*	Alaska	PoW Is. Coffman Cv	T2	Berlese 2	6/14/11		55.9795	-132.86256	101	female , male
UAM:Ento:229946	*C. tlagu*	Alaska	PoW Is. Coffman Cv	T2	pitfall 4	7/27/11	8/7/11	55.9795	-132.86256	101	female
UAM:Ento:229944	*C. tlagu*	Alaska	PoW Is. Hatchery Ck.1	OG	Berlese	8/9/11		55.92444	-132.93938	4	female
UAM:Ento:142985	*C. tlagu*	Alaska	PoW Is. Hatchery Ck.4	OG	pitfall 2	5/14/10	5/30/10	55.88602	-132.8607	11	female
UAM:Ento:142986 *	*C. tlagu*	Alaska	PoW Is. Hatchery Ck.4	T2	pitfall 3	5/30/10	6/14/10	55.88433	-132.89734	26	male
UAM:Ento:204239	*C. tlagu*	Alaska	PoW Is. Hatchery Ck.4	OG	pitfall 2	5/31/11	6/14/11	55.88602	-132.8607	11	male
UAM:Ento:217990	*C. tlagu*	Alaska	PoW Is. Hatchery Ck.4	OG	pitfall 3	6/28/11	7/12/11	55.88602	-132.8607	11	male
UAM:Ento:221708	*C. tlagu*	Alaska	PoW Is. Hatchery Ck.4	2	Berlese 5	7/27/11		55.88285	-132.89795	27	female
UAM:Ento:203237	*C. tlagu*	Alaska	PoW Is. Luck Lk. 1 Rd.	OG	pitfall 4	5/24/11	6/5/11	55.97805	-132.75456	10	female
UAM:Ento:216180	*C. tlagu*	Alaska	PoW Is. Luck Lk. 1 Rd.	OG	pitfall 4	6/21/11	7/6/11	55.97805	-132.75456	10	male
UAM:Ento:154335	*C. tlagu*	Alaska	PoW Is. Luck Lk. 2 Rd.	OG	pitfall 1	7/8/10	7/30/10	55.96855	-132.75615	10	female
UAM:Ento:203238	*C. tlagu*	Alaska	PoW Is. Luck Lk. 2 Rd.	OG	pitfall 3	5/24/11	6/5/11	55.96855	-132.75615	10	male
UAM:Ento:159119	*C. tlagu*	Alaska	PoW Is. Luck Lk. 3 Rd.	OG	Berlese 4	7/29/10		55.95347	-132.7708	5	female
UAM:Ento:203239	*C. tlagu*	Alaska	PoW Is. Luck Lk. 3 Rd.	OG	Berlese 1	6/5/11		55.95347	-132.7708	5	female
UAM:Ento:133943	*C. tlagu*	Alaska	PoW Is. Luck Point	CC	Berlese 2	5/21/10		55.98497	-132.787	25	male
UAM:Ento:159120	*C. tlagu*	Alaska	PoW Is. Luck Point	CC	pitfall 1	7/9/10	8/1/10	55.97953	-132.77156	24	female

Table 14. Continued.

UAM:Ento:167053	*C. tlagu*	Alaska	PoW Is. Luck Point	CC	pitfall 1	8/1/10	8/11/10	55.97953	-132.77156	24	male
UAM:Ento:203011	*C. tlagu*	Alaska	PoW Is. Luck Point	T2	pitfall 1	5/23/11	6/5/11	55.98261	-132.77986	6	female
UAM:Ento:229942	*C. tlagu*	Alaska	PoW Is. Luck Point	CC	pitfall 1	8/2/11	8/9/11	55.97953	-132.77156	24	female
UAM:Ento:229943	*C. tlagu*	Alaska	PoW Is. Luck Point	CC	Lindgren	8/2/11	8/9/11	55.97939	-132.77216	25	male
UAM:Ento:121024	*C. tlagu*	Alaska	PoW Is. Staney Ck.	CCe	pitfall	4/27/10	5/15/10	55.87126	-133.06697	5	male
UAM:Ento:202344	*C. tlagu*	Alaska	PoW Is. Staney Ck.	CC	pitfall 3	5/16/11	5/31/11	55.872	-133.06523	26	male
UAM:Ento:229945	*C. tlagu*	Alaska	PoW Is. Staney Ck.	OG	pitfall 4	7/12/11	7/27/11	55.79901	-133.11782	20	male
UAM:Ento:230091	*C. tlagu*	Alaska	PoW Is. Staney Ck.	OG	pitfall 2	5/14/12	5/28/12	55.79901	-133.11782	20	female
UAM:Ento:231726	*C. tlagu*	Alaska	PoW Is. nr Black Lk	AH	pitfall	7/9/11	7/10/11	55.58818	-132.88881	2	male
UAM:Ento:231727	*C. tlagu*	Alaska	PoW Is. nr Black Lk	AH	pitfall	7/9/11	7/10/11	55.58818	-132.88881	2	female
UAM:Ento:235023	*C. tlagu*	Alaska	PoW Is. Hatchery Ck.4	OG	pitfall	5/15/12	5/28/12	55.88602	-132.8607	11	female
UAM:Ento:235024	*C. tlagu*	Alaska	PoW Is. Luck Point	CC	Berlese	5/31/12		55.98497	-132.787	25	female
UAM:Ento:235025	*C. tlagu*	Alaska	PoW Is. Luck Lk. 1 Rd.	OG	pitfall	5/16/12	5/31/12	55.97805	-132.75456	10	female
UAM:Ento:235026	*C. tlagu*	Alaska	PoW Is. Luck Lk. 3 Rd.	OG	Berlese	5/22/12		55.95347	55.95347	5	male
UAM:Ento:230088	*C. dectes*	Oregon	Mary's Peak		w-screen Berlese	10/30/12		44.50413	-123.55125	5000	female , male
UAM:Ento:228458	*C. dectes*	WA	Lewis Co.		Berlese	5/6/78		46.62848	-122.27701	5000	male , female
UAM:Ento:228446	*C. dectes*	Oregon	Marys Peak		w-screen	5/11/12		44.50413	-123.55125	5000	larva
UAM:Ento:228447	*C. dectes*	Oregon	Marys Peak		w-screen	5/11/12		44.50413	-123.55125	5000	larva
UAM:Ento:228448	*C. dectes*	Oregon	Marys Peak		w-screen	5/11/12		44.50413	-123.55125	5000	larva
UAM:Ento:228449	*C. dectes*	Oregon	Marys Peak		w-screen	5/11/12		44.50413	-123.55125	5000	larva
UAM:Ento:228450	*C. dectes*	Oregon	Marys Peak		w-screen	5/11/12		44.50413	-123.55125	5000	larva
UAM:Ento:228451	*C. dectes*	Oregon	Marys Peak		w-screen	5/11/12		44.50413	-123.55125	5000	larva
UAM:Ento:228452	*C. dectes*	Oregon	Marys Peak		w-screen	5/11/12		44.50413	-123.55125	5000	larva
UAM:Ento:228453	*C. dectes*	Oregon	Marys Peak		w-screen	5/11/12		44.50413	-123.55125	5000	larva
UAM:Ento:228454	*C. dectes*	Oregon	Marys Peak		w-screen	5/11/12		44.50413	-123.55125	5000	larva
UAM:Ento:228455	*C. dectes*	Oregon	Marys Peak		w-screen	5/11/12		44.50413	-123.55125	5000	larva
UAM:Ento:228456	*C. dectes*	Oregon	Marys Peak		w-screen	5/11/12		44.50413	-123.55125	5000	larva
UAM:Ento:228457	*C. dectes*	Oregon	Marys Peak		w-screen	5/11/12		44.50413	-123.55125	5000	larva
UAMObs:Ento:228643	*C. dectes*	Oregon	Cape Lookout			11/6/12		45.33954	-123.99289	5000	male
UAM:Ento:234931	*C. dectes*	Oregon	Cape Lookout			11/6/12		45.33954	-123.99289	5000	male

DNA sequencing. Adult specimens and larvae designated for DNA extraction were stored at -70°F in cryovials containing 100% EtOH. Specimen data are presented in Table 1. DNA was extracted from whole bodies of five adult specimens from the Alaskan population and from seven whole bodies of the Oregon larvae. During the extraction process, specimens were opened with a pin prick to allow full extraction of DNA from soft tissues. After extraction was complete, specimens were soaked overnight in 70% EtOH to stop further deterioration of specimen exoskeletons in order to preserve them for future morphological study. Extractions were performed using a Qiagen DNeasy© blood and tissue extraction kit which was used according to the spin-column protocol for animal tissues. To amplify the COII gene, the following primer pair was used: forward COII-2a (ATAGAKCWTCYCCHTTAATAGAACA) and reverse COII-9b (GTACTTGCTTTCAGTCATCTWATG) taken from Whiting (2002).

Upon completion, extraction success was tested using a nano-drop spectrophotometer. DNA concentrations were (0.5–4.0 ng/μL). Primers were diluted at a relatively high concentration of 10μM in accordance with Whiting (2002). PCR was performed using the following 25μl PCR-mix: 12.5μl GoTaq DNA polymerase, 1μl each of the forward and reverse primers, 1μl Mg+, 9.75μL DNA-grade distilled water and 1μL template DNA. The following cycling regime was applied: (1) 1 min at 95°C, followed by (2) 35 cycles of 1 min at 95°C, 1 min at 59°C, and 1 min at 72°C, and (3) a final extension of 7 min at 72°C. Amplification success and correct band length was confirmed visually on an agarose gel stained with ethidium bromide. Bi-directional sequencing was performed at the University of Washington's High Throughput Genomics Unit.

Alignment. Sequences were aligned using CodonCode Aligner v4.0.4 (http://www.codoncode.com/aligner/) and proofread by eye with reference to codon position and the inferred amino acid sequence based on Liu and Beckenbach (1992). Alignment was without difficulty due to the absence of indels within the protein-coding sequence. MacClade was used to produce a consensus of forward and reverse reads (Maddison & Maddison, 2005).

Model Selection. JModelTest v2.1.3 (Darriba et al. 2012, Guindon and Gascuel 2003) was used to determine the best fitting model among 88 available for testing. The AIC, BIC and DT all chose the model HKY+G as the best fit for the data.

Analysis. Bayesian analyses were conducted using MrBayes v3.2 (Ronquist and Huelsenbeck 2003) under the HKY+G model with default priors. Two simultaneous MCMC runs with four chains each (3 hot and 1 cold) were performed for 10 million generations and sampled every 1, 000 steps discarding a burnin of 25%. To evaluate whether the MCMC analysis had reached stationarity, trace files were examined in Tracer v1.5 (Rambaut & Drummond, 2003). These showed signs of good mixing and had plateaued at equal values. The average standard deviation of split frequencies between the two runs had dropped below 0.01 by 12% of the 10M step run, also indicating both runs had converged. Maximum Likelihood analyses were conducted using Garli v.2.0.1019 (Zwickl, 2006) under the HKY+G model with 1000 non-parametric bootstrap search replicates in addition to a non-bootstrap analysis of 100 search replicates from random starting trees.

Collecting methods and results. Specimens of this new species were collected primarily using pitfall traps and Berlese funnels (Table 14) as part of our four year, ongoing project investigating forestry practices in the Tongass National Forest (Fig. 8). Two specimens were caught in a very different habitat in pitfall traps set on a transect of 20 traps spaced 100m apart in a treeless alpine zone (917m elevation) near Black lake, Prince of Wales Isl., with tundra-alpine-heath vegetation (e.g. *Harrimanella stelleriana*, *Luetkea pectinata*, *Rhytidiadelphus loreus*). This collection was part of a rapid biotic assessment of Southeast Alaska alpine zones (Fig. 8) and was located 45 km southwest of the Coffman Cove collection sites. Pitfall traps consisted of paired (Coffman Cove) or single (alpine) plastic cups 8.3 cm in diameter and 7.5 cm deep filled 1/2–2/3 with non-toxic propylene glycol based antifreeze, Sierra © brand (Coffman Cove), or soapy water (alpine) with rain-roofs ~3 cm from the ground above the traps. Traps were emptied once every two weeks (Coffman Cove) or daily (alpine zone). Paired traps were 30cm apart with a plastic ruler embedded in the ground between them to act as a barrier to divert arthropods into the traps. As part of the Tongass sampling, BioQuip © collapsible Berlese funnels were used with ~ $1m^2$ of leaf/moss litter sifted prior to running under 40 watt bulbs for 48h. These methods resulted in 37 specimens collected. However, incredible effort was involved. A total of 1, 136 pitfall trap and 284 Berlese samples were processed from 2010 and 2011 that have generated 10, 218 beetle specimens to date. The alpine sampling involved 83 pitfall trap samples, which yielded two *Caurinus* specimens. Twenty-six *Caurinus* specimens were captured in pitfall traps, ten in Berlese funnels, and one, surprisingly, in a Lindgren

funnel. Great care was taken to ensure pitfall trap rims were at or below the level of the ground – certainly an important factor when trapping an animal ~ 2 mm in size.

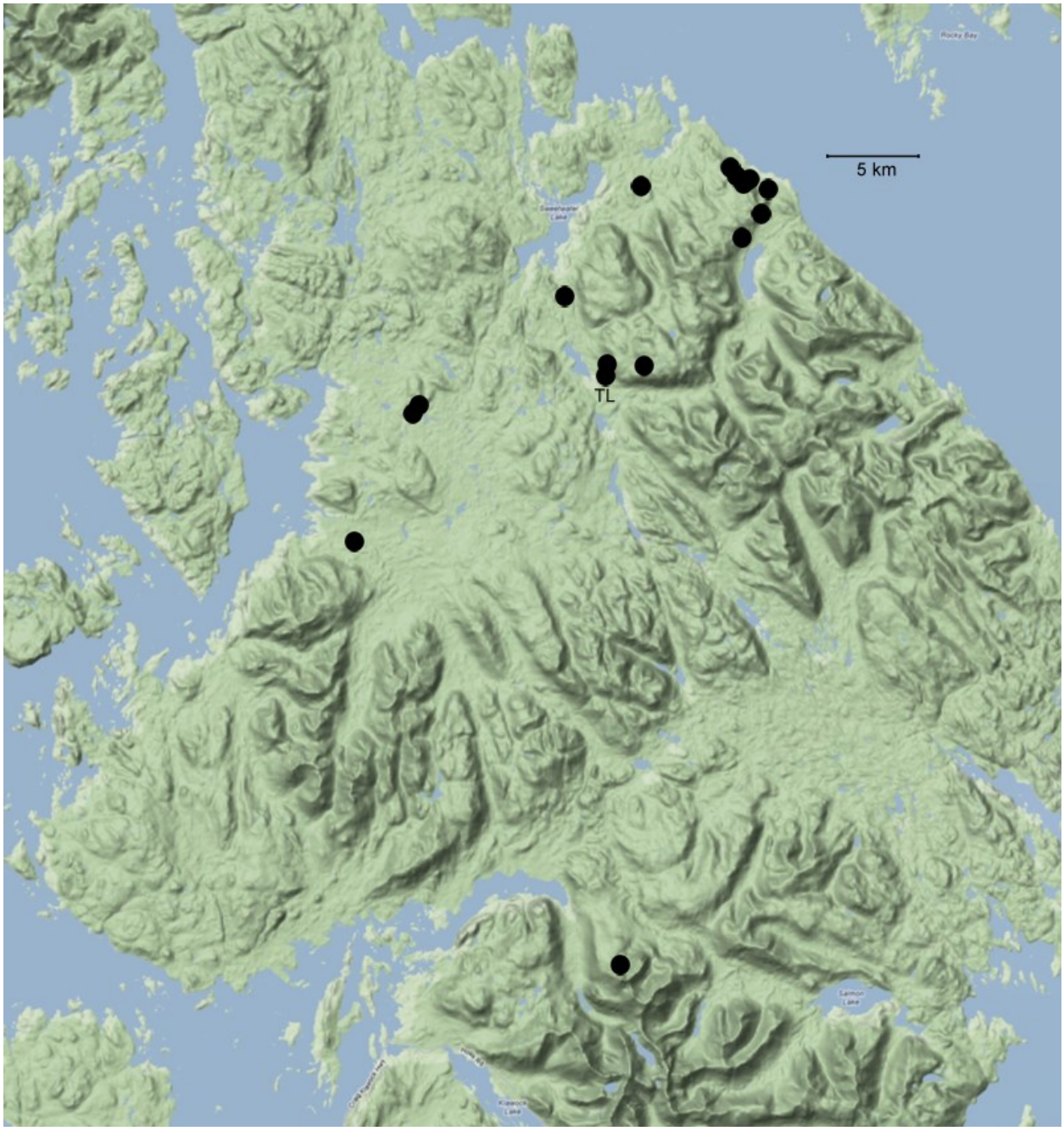

Figure 8. Sixteen sites at which *Caurinus tlagu* specimens were found, north end of Prince of Wales Island, Alaska. Table 1 lists site and specimen data, also available online at http://arctos.database.museum/saved/Caurinus-AK. TL = type locality.

The majority of specimens (35/37) were collected in perhumid rainforest dominated by Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), lodgepole pine (*Pinus contorta* var. *contorta*), Alaska yellow cedar (*Chamaecyparis nootkatensis*), red cedar (*Thuja plicata*), and red alder (*Alnus rubra*) (Fig. 9). Of 24 sites sampled in the Tongass National Forest project, *Caurinus* was found in 14 sites. Fifteen specimens were found in six of six sampled old growth sites, eleven in three of six sampled thinned secondary growth sites, seven in four of six sampled clear cuts, and one in one of six sampled unthinned secondary growth sites. One additional specimen was found in an ecotone next to a clear cut that was not part of the 24 structured sampling sites. The null hypothesis of *Caurinus* being equally trappable in all four habitat types: old growth, thinned secondary growth, unthinned secondary growth, and clear cuts, (ignoring the ecotone), is rejected ($Chi^2 = 12.59$, df=3, P=0.0056). These animals are less trappable in unthinned secondary growth sites than expected under the null, and more trappable in old growth and thinned secondary growth sites than expected under the null.

Figure 9. Habitats of *Caurinus tlagu* **A** Habtiat of type locality, thinned secondary growth with 18 ft. spacing between trees, 55.88433, -132.89734 **B** example of old growth habitat in which specimen UAM:Ento:204239 was found, 55.88602,-132.8607 **C** example of clearcut, a habitat type in which seven specimens were found, 55.872, -133.06523 **D** example of treeless, alpine heath – tundra in which two specimens were found, 55.58818, -132.88881.

Results from molecular analyses

DNA sequence characteristics. The final alignment of the DNA sequences (11 *Caurinus* sequences, 2 outgroup *Boreus* sequences) was 639 base pairs long with 491 constant sites, 21 variable but parsimony-uniformative sites, and 127 parsimony informative sites. Among the *Caurinus* sequences there were 604 constant sites and 35 parsimony informative sites. Of these 35 variable sites between the *Caurinus* species, 34 were binary with all specimens of each species sharing the same base differing from the other species. As expected, most (29) of these variable sites were third codon positions, with six variable first codon position sites, and zero variable second codon position sites. The null hypothesis of homogeneity of base frequencies across taxa was not rejected by a Chi-square test performed in PAUP*4.0b10 (Chi^2=27.5, df=36, P=0.85) (Swofford, 2003). These sequences are available from Genbank (accession numbers KF282717 through KF282727) and the aligned NEXUS and tree files are available from TreeBase (http://purl.org/phylo/treebase/phylows/study/TB2:S14415) under study Accession number 14415.

The *Caurinus* species are 98.5% identical in their inferred COII amino acid sequences (209 of 212 amino acids are identical). The three amino acid replacements are as follows: The 113th site of the amino acid translation is an Alanine (nonpolar) shared by all seven *Caurinus dectes* specimens but is a Threonine (polar) in all five *Caurinus tlagu* specimens; at the 114th site an Aspartic acid (acid polar) shared by all seven *Caurinus dectes* specimens is a Asparagine (polar) in all five *Caurinus tlagu*

specimens; and at the 148th site an Isoleucine (nonpolar) shared by all seven *Caurinus dectes* specimens is a Valine (nonpolar) in all five *Caurinus tlagu* specimens.

All seven *Caurinus dectes* share identical COII nucleotide sequences whereas only three of the *Caurinus tlagu* share identical sequences, the fourth *Caurinus tlagu* differs at one site (0.156% divergent) from the other three *Caurinus tlagu*. The two *Caurinus* species are 5.44% divergent from each other (uncorrected "p" distance). The two outgroup species are 3.9% divergent from each other, and 21% (*Boreus hyemalis*) to 20% (*Boreus westwoodi*) divergent from *Caurinus*. The COII GenBank record of *Caurinus dectes* (AF424001.1) is 21.7% divergent from the seven *Caurinus dectes* we sequenced. Using the parameter values from the Garli analysis (see below) to set the HKY+G model in PAUP*4.0b10 allowed the estimation of distances corrected for multiple hits: the two *Caurinus* species are 7.17% divergent from each other. The two outgroup species are 5.6% divergent from each other, and 106.7% (*Boreus hyemalis*) to 103.5% (*Boreus westwoodi*) divergent from *Caurinus*.

Bayesian Analysis. Tracer reported auto-correlation times of 1027 and 1015 for the two runs with Effective Sample Sizes for all parameters of each run above 7000 (with samples from both runs combined, the ESS of each parameter was above 15, 000). Parameter estimates of both runs combined were as follows: the harmonic mean of the estimated marginal likelihood was –1515.7, tree length 0.692, the transition/transversion rate ratio (kappa) 6.59, pi(A) 0.356, pi(C) 0.151, pi(G) 0.102, and pi(T) 0.391 with the alpha shape parameter at 0.258.

Garli Analysis. The 1000 bootstrap replicate analysis resulted in similarly strong branch support values as the Bayesian analysis (Fig. 10). One hundred non-bootstrap replicates were completed, the best tree of which was found in 96 of the searches and was identical in topology to the Bayesian tree (Fig. 10) with a -lnL of 1476.75, tree length of 0.858, and parameter values of: K parameter 8.789, ti/tv 3.321, pi(A) 0.3596, pi(C) 0.1481, pi(G) 0.0991, and pi(T) 0.3933 with the alpha shape parameter at 0.1733.

Both the Bayesian and maximum likelihood analyses found strong support for reciprocal monophyly of both *Caurinus* species (Fig. 10).

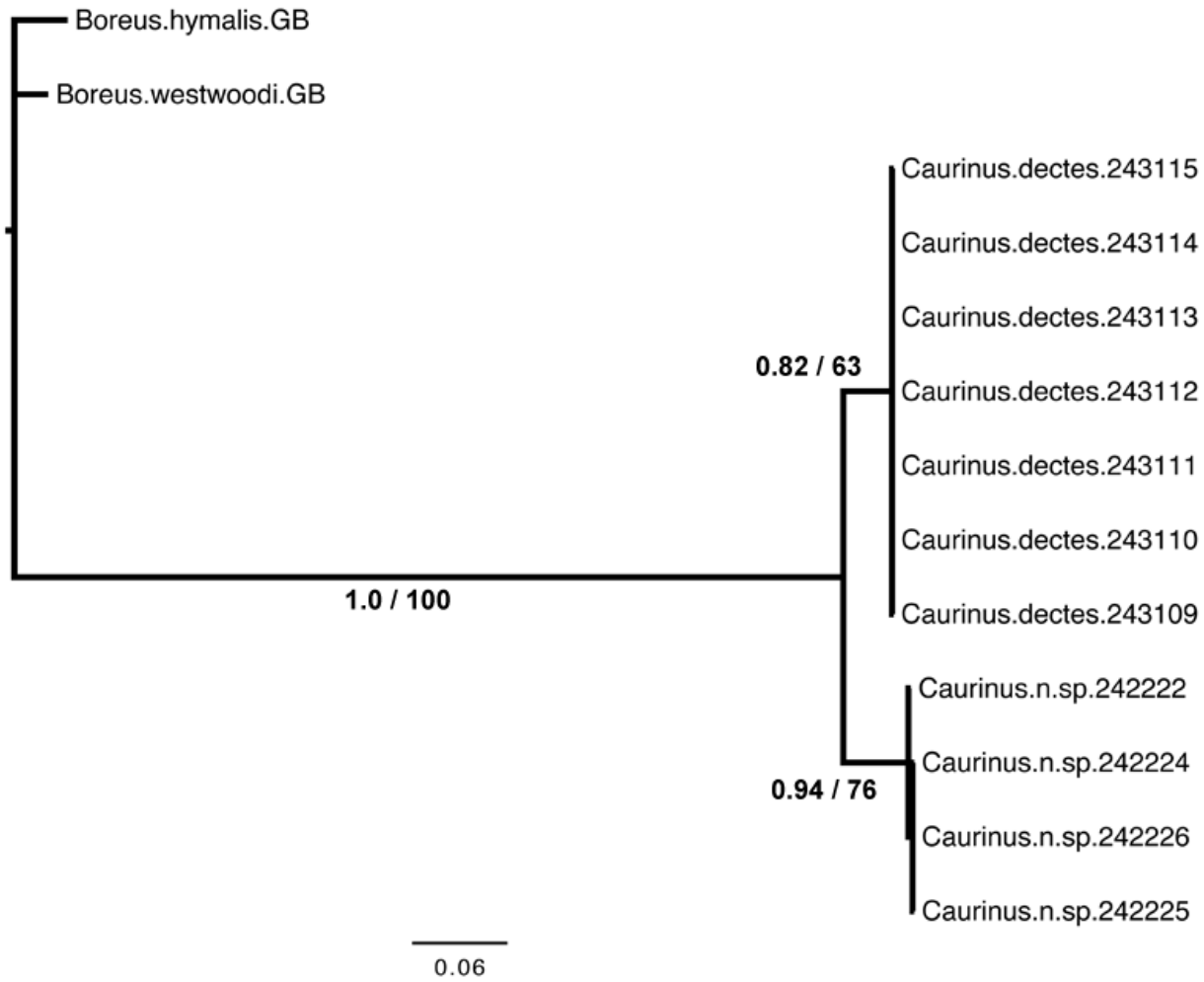

Figure 10. Inferred phylogeny from Bayesian analysis. Each terminal is a single specimen with the UAM cryovial barcode of its DNA extraction indicated by a six digit number. Branch support is indicated as estimated posterior probability from the Bayesian analysis first and maximum-likelihood bootstrap percentages second. Branch lengths are proportional to the number of substitutions per site as reconstructed by MrBayes 3.2. Specimen 242224 is the holotype of *Caurinus tlagu* http://arctos.database.museum/guid/UAM:Ento:142986. The remaining three *C. tlagu* specimens correspond to the following paratypes in Table 1: 242222 (UAM:Ento:135818), 242225 (UAM:Ento:159119), and 242226 (UAM:Ento:154335).

Systematics

Caurinus tlagu Sikes & Stockbridge, sp. n.
urn:lsid:zoobank.org:act:BFFF780A-737D-4187-8539-32270D80D4C5
http://species-id.net/wiki/Caurinus_tlagu

Holotype. Male (in UAM), here designated, labeled "USA: Alaska, Prince of Wales Is. Hatchery Ck.4, 30 May-14 June 2010, 55.88433°N, 132.89734°W ± 26m, 82m elev., thinned secondary growth with 18 ft. spacing between trees, pitfall 3, J. Stockbridge, C. Bickford", / "HOLOTYPE *Caurinus tlagu* Sikes & Stockbridge 2013 UAM:Ento:142986" [red paper]. http://dx.doi.org/10.7299/X7GH9J4M

Paratypes. 36 Specimens (Table 14). The following 17 paratypes will be deposited in the collections indicated: male UAM:Ento:159146, female UAM:Ento:142985, female UAM:Ento:235025 (CAS); male UAM:Ento:229945, female UAM:Ento:235024, female UAM:Ento:229942 (OSAC); male UAM:Ento:235026, female UAM:Ento:203239, female UAM:Ento:203011 (PMJ); male UAM:Ento:167053, female UAM:Ento:229944, female UAM:Ento:235023 (SEMC); male UAM:Ento:217990, female UAM:Ento:221708, female UAM:Ento:159120 (USNM); male UAM:Ento:229943, female UAM:Ento:230091 (MTEC), and the 19 remaining in UAM.

Type Locality. USA: Alaska, Prince of Wales Is. Hatchery Ck, 55.88433°N, 132.89734°W ± 26m, 82m elev. (Fig. 8, 9A).

Measurements. Restricted to specimens with retracted genitalia (3 males, 10 females), length, min. – max., mean ± SD: male 1.58–2.02, 1.74 ± 0.24 mm, female 1.64 – 2.00, 1.79 ± 0.13 mm.

Diagnosis. Circumference of eye of males comprises 31-35 (n=3) ommatidia (*Caurinus dectes* males have 38–39, n=3). Scanning electron microscope-level resolution is required to obtain reliable counts (Fig. 11). Female 8th sterna without a median notch (n=10), or with a shallow median notch (n=5) (Fig. 12A, C, 13C, D). *Caurinus dectes* females have a shallow median notch or a pronounced median notch (Fig. 5B; see also Russell, 1979b; Fig. 10). This is visible at 40× and higher magnification.

Description. Body length 1.5–2.3 mm, flea-like in lateral view, color reddish brown, sparsely pubescent, strongly sclerotized (Fig. 13). Rostrum absent or reduced. Clypeolabral suture present. Clypeus divided into post and anteclypeus. Penultimate maxillary palpomere enlarged and club shaped. Antennal insertion lateral, widely separated. Ocelli absent. Antennae with sixteen antennomeres and a single countersunk sensilla on antennomeres 4, 5, and 6 (Fig. 14). Mandible with two subapical teeth (Fig. 13B). Male forewings extend to end of first abdominal segment, with six bristles (Fig. 15A), hindwings absent. Female forewings pad-like, hindwings absent. Tarsi five segmented, tarsal claws present. Pilosity absent. Abdomen widest at segments 4 and 5, segments 2-6 fused, annular. Male 8th tergum and sternum not fused. Male 9th tergum and sternum not fused. Genitalia normally concealed in both sexes. Male gonostyles flattened, deeply incised (Fig. 15B).

Variation. One male (UAM:Ento:231726) has 7 bristles on its right wing, as a result of a very small extra basal bristle, and six on its left.

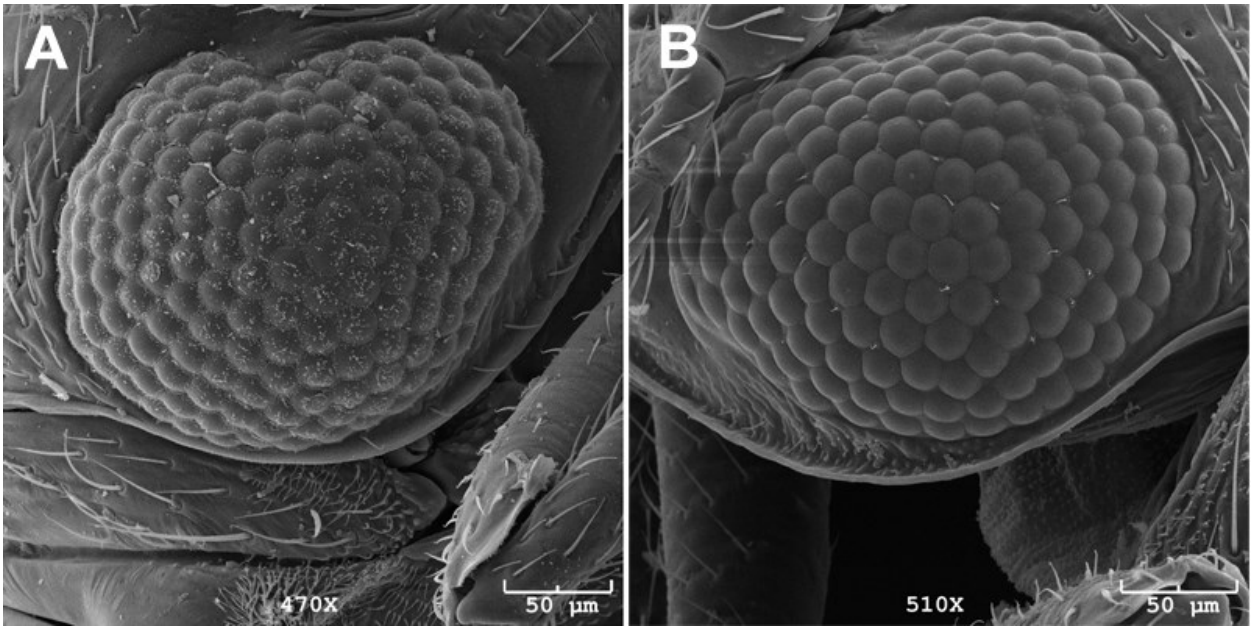

Figure 11. Comparison of ommatidia. Eye of **A** male *Caurinus dectes* (UAM:Ento:230088) showing 38 ommatidia around circumference of right eye, dorsal is to the left, and **B** male *Caurnius tlagu* (UAM:Ento:202344) showing 35 ommatidia around circumference of left eye, dorsal is to the right. Scale bar = 50 µm.

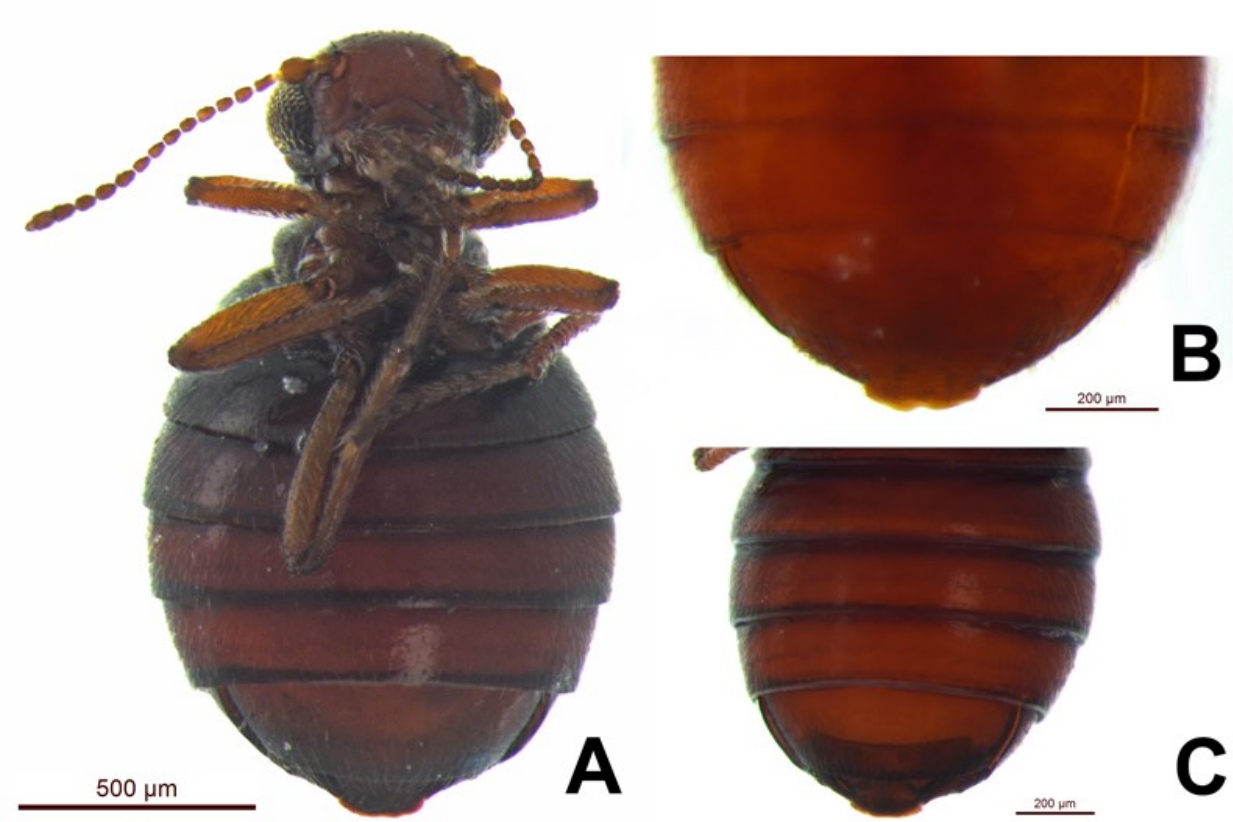

Figure 12. Comparison of 8th abdominal sternum. **A** ventral view of female *Caurinus tlagu* (UAM:Ento:203239) showing 8th sternum with shallow median emargination / notch, scale bar = 500 µm **B** ventral view of abdomen of female *Caurinus dectes* (UAM:Ento:228458) showing 8th sternum with a pronounced notch, scale bar = 200 µm **C** ventral view of abdomen of female *Caurinus tlagu* (UAM:Ento:203011) showing 8th sternum with shallow emargination / notch, scale bar = 200 µm.

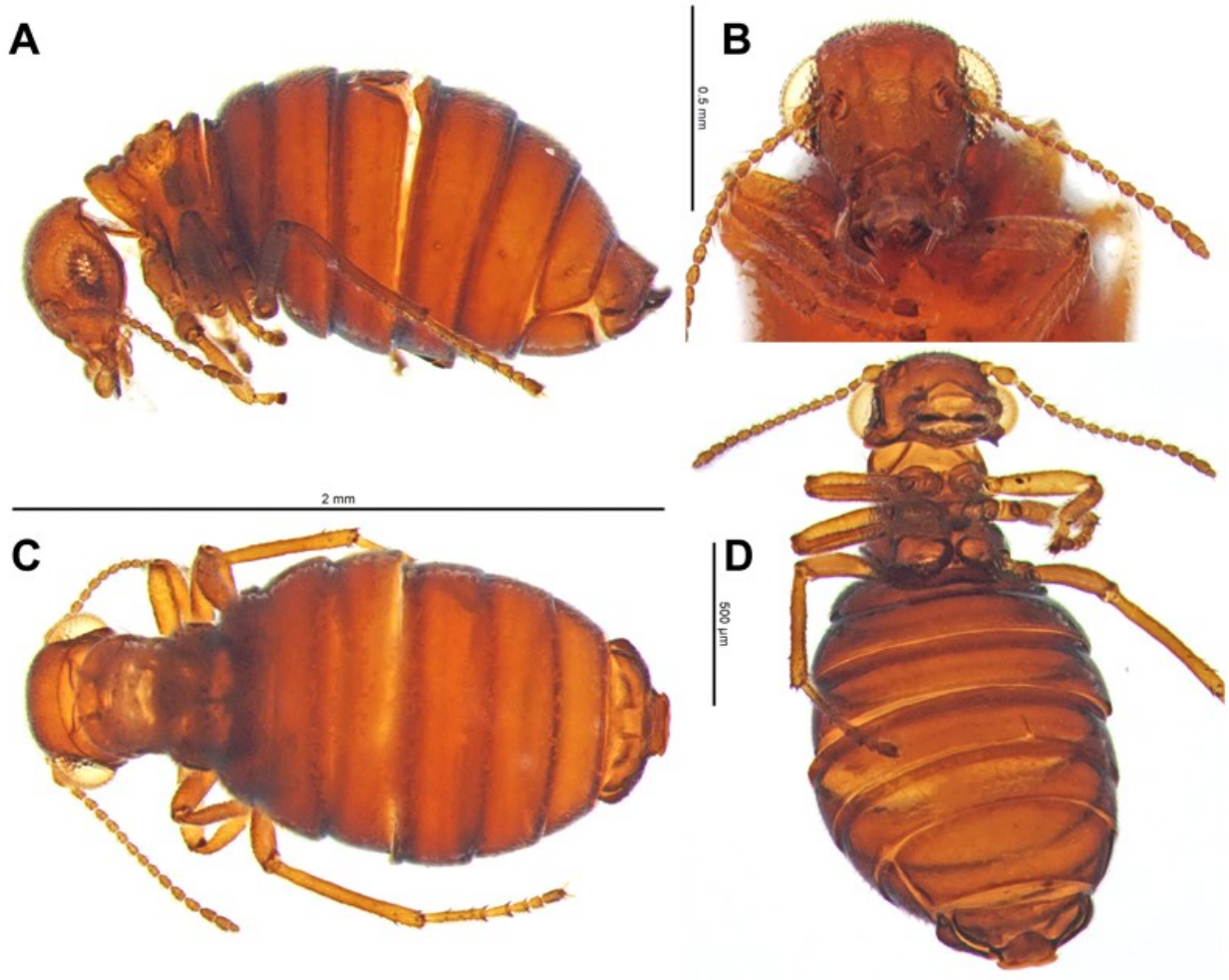

Figure 13. Female *Caurinus tlagu* (UAM:Ento:159119) that had been cleared in KOH. **A** lateral view (broken abdomen), scale bar = 2 mm **B** face, scale bar = 0.5 mm **C** dorsal view, scale bar = 2 mm **D** ventral view, scale bar = 0.5 mm.

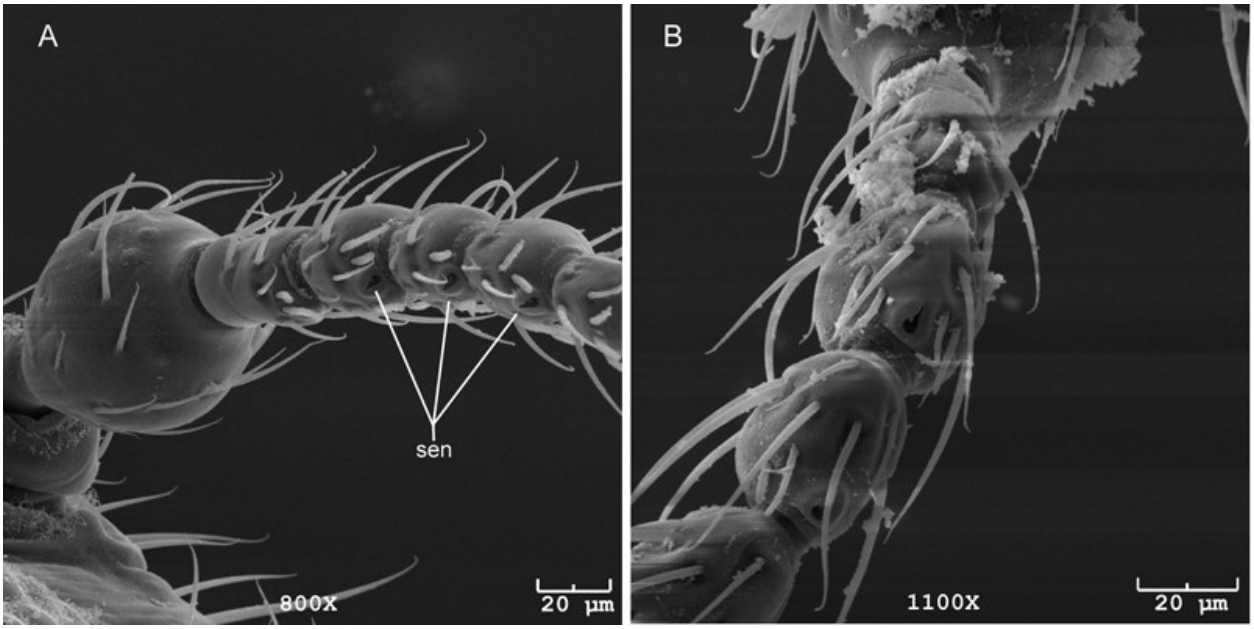

Figure 14. Base of *Caurinus* antenna showing sensilla on antenomeres 4, 5, and 6. **A** female *Caurinus dectes* (UAM:Ento:230088), **B** female *C. tlagu* (UAM:Ento:203237); sen = sensilla, scale bars = 20 µm.

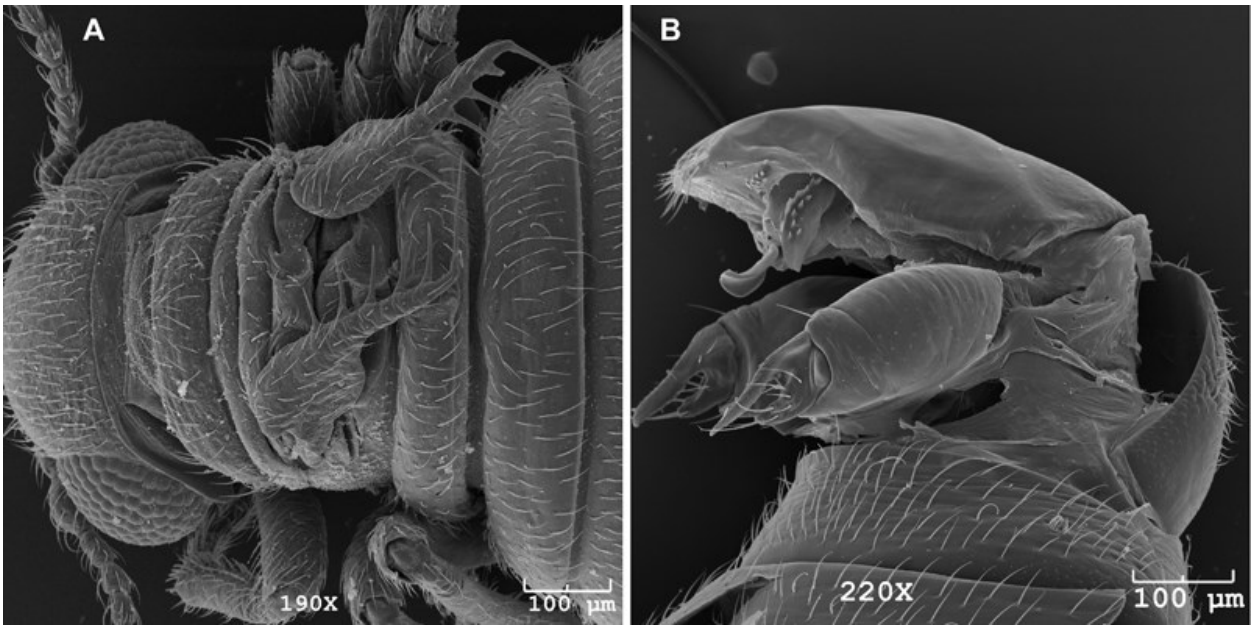

Figure 15. SEM images of male *Caurinus tlagu* (UAM:Ento:204239), scale bars = 100 µm **A** dorsal view showing wings **B** everted genitalia showing paired gonostyles, oblique lateral view.

Geographic Distribution and Habitat. This species is only known from the northern half of Prince of Wales Island within a region about 45 km in size (Fig. 8). It was collected in forest habitat of various stages: old growth, secondary growth (thinned and unthinned), and young clear cuts; in addition to two specimens caught in alpine heath habitat and one in an ecotone of clearcut / secondary forest. The species is not restricted to lowland forests, nor to old growth forests.

Etymology. "*Tlagu*, " pronounced "tlu-gu, " is derived from the Alaska Native tribal language Tlingit meaning "ancient, forever" (Crippen, 2013) or "old, from the past" (Edwards, 2009). Bierhorst (1985) provided this elaboration: "Among the Tlingit, for example, there are two kinds of stories, *tlagu* (of the long ago) and *ch'kalnik* (it really happened)." We name this species in honor of the place it occurs, its people, and history, in addition to the apparent great age of the genus *Caurinus*.

Discussion

Diagnostic characters were not easily found. These species are very similar phenotypically. The use of ommatidia counts around the circumference of the eyes of males (females we examined overlapped in these counts) is certainly not an ideal character because it is limited to one sex and requires SEM imaging to obtain accurate counts. In part because of this difficulty, and the rarity of specimens, our sample sizes for the assessment of this character are suboptimal. Despite these small sample sizes (n=3 for each species) the means differ significantly based on an unpaired, two-tailed student's t-test ($p = 0.0142$). We hope that ongoing morphological study of the

Mecoptera by Rolf Beutel and others (e.g. Beutel et al., 2008) will better document variation between and within these *Caurinus* species.

During our examination of characters we compared both species for the paired cupuliform and countersunk antennal sensilla described by Beutel et al. (2008, Fig. 3D) as occurring on the distal part of antennomeres 3 and 4. We found these on antennomeres 4, 5, and 6 (Fig. 14) but could not find them on antennomere 3 of either species. Also, we found the countersunk sensillum but not the cupuliform sensillum. We studied 5 specimens of *Caurinus dectes* and 5 of *Caurinus tlagu*, 3 males and 2 females of each, and were able to see sensilla on 2 female *Caurinus dectes* and 1 male and 2 female *Caurinus tlagu* but on no others. A shorter type of setae with a thicker apex is present near the countersunk sensilla (Fig. 14) which were also visible on those specimens on which we did not find sensilla. This lack of confirmation is likely due to the fixed positioning of the specimens for SEM imaging hiding the sensilla from view, although infraspecific variation and absence cannot yet be eliminated as explanations. The lack of sensilla on antennomere 3 of *Caurinus dectes* raises the possibility that there are multiple species under the name *Caurinus dectes*.

We examined the gonostyles of the males (Fig. 15B) for diagnostic characters. These complex structures may still hold diagnostic potential. In particular, the apex of the gonostyle's setose basal tooth appeared tapered in *Caurinus tlagu* and truncate in *Caurinus dectes*. However, we were not able to confirm this state was constant in each species. The shape of the upper blade and the pattern of scale-like ridges on the upper

blade also appeared to differ. Further study indicated these differences were probably due to differences in the available angles of viewing within the SEM.

We do not know the explanation for the very large COII difference (21.7%) seen between the GenBank *Caurinus dectes* record and our own sequences of seven *Caurinus dectes* specimens. Both samples were made by the same collector, and author of the species, L. Russell, from the type locality. The GenBank record for the *Caurinus dectes* COII is 4.5% different from that of the GenBank record for *Panorpa debilis* (AF424023.1) from the same study (Whiting, 2002) which suggests possible contamination or data mixup. Given the ambiguity of the GenBank record's accuracy we decided to exclude it from our analyses.

The two specimens recovered from the treeless alpine tundra site appear to violate characterizations of *Caurinus* being a forest associated lineage. However, *Caurinus dectes* is often recovered from forested and open rocky sites with the common moss *Rhytidiadelphus loreus*, which represented 20% of the total vegetation at the alpine site (K. LaBounty pers. com.). That *Caurinus tlagu* occurs in clear-cuts and secondary growth sites suggests it is not a habitat specialist. However, within the secondary growth sites in which *Caurinus tlagu* was found, it was significantly more common in thinned sites (n= 11) than in unthinned (n=1). The former have been opened by the Forest Service program TWYGS (Tongass Wide Young Growth Studies) in which the trees have been thinned to encourage old-growth conditions whereas the latter habitats are closed-canopy and dark due to the overcrowding of even-aged trees. This does raise questions about the feeding and breeding ecology of *Caurinus tlagu*. Russell

(1979b, 1982) documented *Caurinus dectes* as a specialist on epiphytic and terrestrial leafy liverworts (Jungermanniales). We lack adequate data on the bryophyte communities of the lowland forested sites to assess whether *Caurinus tlagu* shows the same bryophyte associations as *Caurinus dectes*. In particular, seven specimens (19% of our total catch) were found in recently deforested clear cuts, which are likely to have highly disturbed bryophyte communities.

Another notable difference between these *Caurinus* species may be their phenology. Russell (1982) describes adult *Caurinus dectes* as primarily active during the winter (October – April), but reappearing in unseasonably wet, cool weather during the summer. This contrasts with our findings of summer presence of adult *Caurinus tlagu*. Of course, *Caurinus tlagu* could also be active year-round but our sampling regime would fail to detect anything but summer activity.

Various plausible scenarios exist to explain the 1, 059 km range disjunction and presumed allopatric speciation within this genus of wingless mecopterans. Either or both populations could be the result of ancient (paleoendemism) or recent (neoendemism) dispersal from the other population or elsewhere (now extinct, or as yet unfound). Such dispersal could be as simple as the ancient transport of *Caurinus*-laden bryophytes by a bird. Given the genetic divergence between the populations, human transport is unlikely because it would be too recent. Alternatively, and we think more likely, both populations may be relicts of an ancient, and much larger population, with subsequent intervening extinction (paleoendemism). A multi-locus population genetics analysis with incorporation of data regarding the region's geological history would be

needed to test these alternatives. Finally, these animals are not easily found and undetected populations may occur in intervening British Columbia.

Prince of Wales Island was mostly buried under an ice sheet during the maximum of the late Wisconsin glaciation 26,000 to 13,000 ^{14}C years BP (Carrara, Ager, & Baichtal, 2007) and had been repeatedly buried by ice during the Pleistocene. However, considerable biological and geological evidence suggests that ice-free refugia may have existed during this time, allowing many diverse taxa to continue to evolve in relative isolation, and re-seed the region after deglaciation (Carrara et al., 2007). Of 108 mammal species or subspecies occurring in southeastern Alaska, 27 are endemic to the area (Cook et al. 2001). The known locations of *Caurinus tlagu* are in regions that were reconstructed as under ice by Carrara et al. (2007, Fig. 3). Post deglaciation dispersal to these sites from ice-free refugia is the most likely explanation. This suggests, and it would be likely regardless, that *Caurinus tlagu* is more widely distributed than we have documented.

Despite their strong phenotypic similarity, the weight of the evidence supports the conclusion that these separate populations are not conspecific. Their mtDNA sequences being 7.17% divergent (corrected for multiple hits) suggests they have been isolated for probably less than 10 million years (Klicka & Zink, 1997; Papadopoulou, Anastasiou, Vogler, 2010). Regardless, they have probably been isolated for longer than *Boreus westwoodi* and *Boreus hyemalis* have been isolated from each other. This degree of separation eliminates a late Pleistocene (100, 000–250, 000 YBP) speciation event hypothesis. The corrected genetic distances between *Boreus* and *Caurinus* (over

103%), indicate the COII gene is fully saturated with multiple hits at this level of comparison, and support the hypothesis of Russell (1979b) that *Caurinus* is a lineage of great age and not an example of relatively recent evolutionary reversal that would make the Boreinae paraphyletic.

This suggests the split between the genus *Caurinus* and the remaining boreids likely predates the oldest confirmed boreid fossil, *Palaeoboreus zherichini* Sukatsheva & Rasnitsyn, of the Late Jurassic (Grimaldi & Engel, 2005) which appears to be a boreine due to its size and external ovipositor, although it lacks the produced rostrum typical of extant species (Russell pers. com.). If confirmed, such a great age (>145 Ma) for a genus of two extant species would make the lineage an evolutionary relict and its species certainly deserving of conservation attention (Habel & Assmann, 2010; Naskrecki, 2011).

Acknowledgments

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Caurinus dectes specimens. Funding for this project came from two grants to the first author from the Alaska Department of Fish and Game.

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Addendum

During 16–17 May 2013, Loren Russell, the author of *Caurinus dectes* and authority on the ecology of the genus, joined us on Prince of Wales to collect and study *Caurinus tlagu*, and show us how to target its host bryophyte. It took us two years (2010 and 2011) to collect 37 *Caurinus tlagu* specimens using three structured sampling methods at 24 sites. In a few hours of collecting, L. Russell was able to collect over a dozen *Caurinus tlagu* and taught us how to brush them from one of their preferred hosts (*Scapania bolanderi*). A video of L. Russell showing this method is available at https://vimeo.com/68819818 and a second video showing *Caurinus tlagu* hopping is available at https://vimeo.com/68819819. Russell also alerted us to an earlier, ecological study that documented *Caurinus* from the Maybeso Experimental Forest on Prince of Wales Island (LeSage, Merritt, Wipfli, 2005). We were able to confirm that voucher specimens of *Caurinus* from this 2005 study are deposited in the Michigan State University collection.